

FLORAL STRUCTURE, SYSTEMATICS, AND PHYLOGENY IN TROCHODENDRALES¹

PETER K. ENDRESS²

ABSTRACT

Study of the floral structure of *Cercidiphyllum*, *Euptelea*, *Tetracentron*, and *Trochodendron*, at anthesis and in earlier developmental phases, revealed new features of macrosystematic interest. They include the presence of rudimentary tepals in *Trochodendron*, and valvate anther dehiscence, similar exine structure, and similar nectaries on dorsal carpel bulges in *Trochodendron* and *Tetracentron*. These and other similarities point to a close relationship between *Trochodendron* and *Tetracentron*, which together are formally best treated as a family Trochodendraceae. Other new characters, such as zygomorphy or bilateral symmetry of the flowers in early developmental phases and relatively similar anther differentiation, in addition to the established similarities, corroborate the relative homogeneity of the four genera, which can be seen as members of a single order Trochodendrales. The position of this order is intermediate between the Magnoliidae and Hamamelidae so that the formal inclusion of the order in either group can be justified.

The four unusual eastern Asiatic genera *Cercidiphyllum*, *Euptelea*, *Tetracentron*, and *Trochodendron*, with only six species among them are systematically isolated from other dicots, but they form a homogeneous group. This is more or less generally accepted today. In recent classifications they appear in the same order Trochodendrales or at least in the same subclass Hamamelidae. This was not always the case, and their taxonomic history sheds some light on their systematic and phylogenetic significance.

The outstanding combination of characters such as vesselless wood, lack of a perianth, and a special kind of triaperturate pollen make them intermediate between the Magnoliidae and the Rosidae-Hamamelidae. Therefore, the views on the systematic position of the group have oscillated between magnolialian and hamamelidalian affinities.

Siebold and Zuccarini (1839) described the first genus *Trochodendron* and placed it in the Winteraneae. Oliver (1889) described the last of the four genera, *Tetracentron*, and put all of them in the tribe Trochodendreae of the Magnoliaceae.

But Baillon (1871) had already proposed that *Cercidiphyllum* might have affinities with the Hamamelidaceae. Solereder (1899) corroborated this suspicion by extensive morphological work, and Hallier (1901, 1903a, 1903b, 1904) very viv-

idly put forward that Trochodendraceae also are very near the Hamamelidaceae and should even be included in them.

The pendulum swung back with I. W. Bailey and his coworkers, who carefully studied all four genera and firmly established the relationship with the Ranales (Magnoliideae) (Bailey & Nast, 1945; Nast & Bailey, 1945, 1946; Swamy & Bailey, 1949). Pervukhina (1963) and Endress (1969) were of the same opinion after comparative developmental studies of *Trochodendron* and *Euptelea*, respectively.

But the present tendency is to include all four genera in Hamamelidae (Takhtajan, 1964, 1983; Smith, 1972; Cronquist, 1981) (or Hamamelidales sensu Thorne, 1983); *Trochodendron* and *Tetracentron* in Trochodendrales, and *Euptelea* and *Cercidiphyllum* in Hamamelidales (Cronquist, 1981). Dahlgren (1980, but not 1983) placed the four genera in the Trochodendrales. Every genus is in a separate family or even in a separate order (as in Takhtajan, 1983).

Thus, the gross systematic history from the beginning until now shows a change in the emphasis from magnolialian to hamamelidalian affinities. Both are somewhat one-sided positions, because there are clearly affinities to both groups, and the new results presented here corroborate this view. However, for purposes of classification

¹ I thank B. L. Burt, Royal Botanic Garden, Edinburgh, for providing fixed material of *Tetracentron sinense*, and U. Jauch, Institut für Pflanzenbiologie, University of Zürich, R. Siegrist, and A. Zuppiger for technical collaboration. I am grateful for valuable comments on the manuscript by Nancy R. Morin, Rudolf Schmid, and Shirley C. Tucker.

² Institut für Systematische Botanik der Universität Zürich, Zollikerstrasse 107, 8008 Zürich, Switzerland.

it is necessary to place them in only one of the groups, but placement either way can be about equally justified.

MATERIALS AND METHODS

The following collections, all cultivated material, were used for this investigation:

Cercidiphyllum japonicum Hoffmann et Schultes, male, *Endress* 6687 (dat. div., 1984); female, *Endress* 6688 (dat. div., 1984), old Botanical Garden, University of Zürich.

Euptelea polyandra Sieb. et Zucc., *Endress* 516 (dat. div., 1967–1968), Eidgenössische Forschungsanstalt für Obst-, Wein- und Gartenbau, Wädenswil (Figs. 3, 32, 40, 44, 58, 59); *Endress* 6686 (dat. div., 1984), Botanical Garden, University of Zürich (all other figures).

Tetracentron sinense Oliver (8 June 1976, 10 Aug. 1976), Royal Botanic Garden, Edinburgh.

Trochodendron aralioides Sieb. et Zucc., *Endress* 6684 (dat. div., 1984), Botanical Garden, University of Zürich.

All material is deposited in Zürich (Z). Figures 32 and 40, where only the generic name is mentioned, are both based on these species and specimens.

Flowers at anthesis and in various developmental stages were observed in the living state (except *Tetracentron*). Material fixed in FAA of all four genera was studied with serial microtome sections stained with safranin and astra-blue and with the scanning electron microscope after treatment with the critical-point drying and Au/Pd-sputtering methods.

RESULTS

THE FLOWERING SHOOT AT ANTHESIS

There is a differentiation in long and short shoots with inflorescences produced only on short shoots, except in *Trochodendron*. This differentiation is most extreme in *Cercidiphyllum* and *Tetracentron*, both having short shoots with a single foliage leaf.

Trochodendron. An upright cluster of 10–30 yellowish green bisexual flowers (ca. 1 cm diam.) (Fig. 1) with long pedicels appears in late spring while the shoots are expanding. Flowers observed in the Botanical Garden at Zürich in 1980 became visible between the bud scales and leaves in early May. On 12 May the flowers were all exposed, on 22 May open nectar was present between the stamens and styles on the ovary sur-

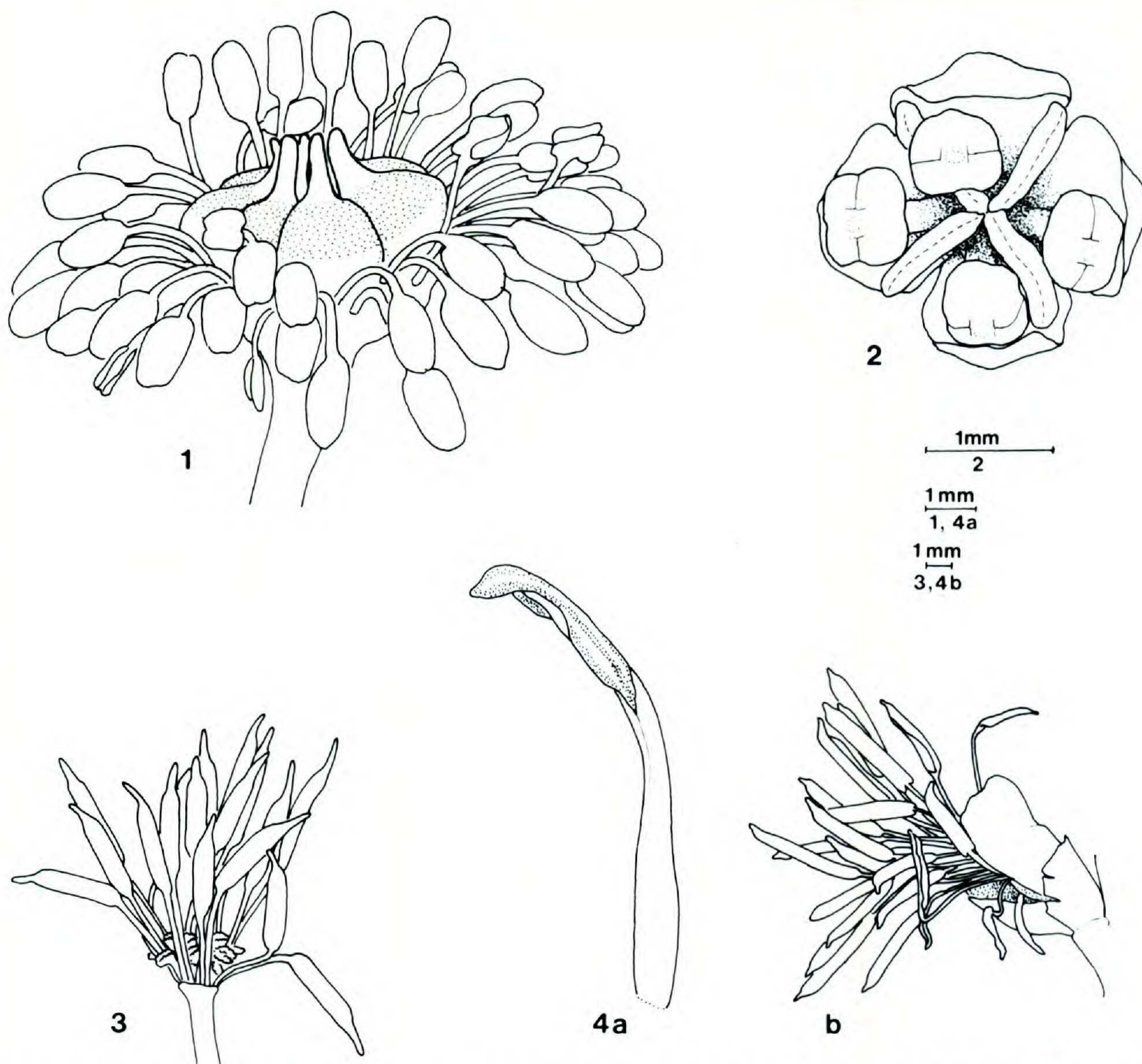
face, but all anthers were still closed. On 28 May the first stamens were open and contained sticky pollen; dry remains of nectar were still present. During the period when they were fully exposed, the open flowers enlarged from about 0.8 to 1.2 cm diam.

Since mature fruits regularly developed from that plant, the flowers seem to be bisexual (or the development may be apomictic). The flowers seem to be proterogynous. There is no sign of androdioecism in contrast to the observation of Keng (1959) on plants in Taiwan. The floral character syndrome points to myophily (or unspecialized entomophily). Keng (1959) observed bees and butterflies as visitors of the sweet-scented flowers in mid-April 1957 in Taiwan.

Tetracentron. About a hundred very small yellowish bisexual flowers (2 mm diam.) (Fig. 2) are sessile on a long stiff axis. The studied material, cultivated in Edinburgh, flowered in late summer (August 1976). A secretory surface that apparently also secretes nectar is at the same site as in *Trochodendron*. Presumably the flowers are also myophilous (Takhtajan 1969; Cronquist 1981: anemophilous).

Euptelea. A cluster of 6–12 (Smith, 1946) pendent inconspicuous bisexual pedicelled flowers with many stamens and carpels (Fig. 3) is produced by each flowering shoot. In the closed state the long anthers are red, but brownish when open. Pollen is dry and powdery. The minute carpels expose the white stigmatic papillae between the filament bases. No nectar is produced. In contrast to *Trochodendron*, anthesis is short and takes place in early spring (March or April at Zürich) before the young leaves expand. Thus, *Euptelea* exhibits an anemophilous character syndrome. *Euptelea polyandra* is presumably at least partly self-incompatible. Two neighboring specimens cultivated in the Botanical Garden at Zürich regularly set copious fruit, but other plants cultivated in isolation produce few or no fruits.

Cercidiphyllum. This is the only genus of Trochodendrales with unisexual flowers (in dioecious distribution). The inconspicuous female inflorescences consist of two to seven (Spongberg, 1979) unisexual flowers with big red stigmas (Fig. 4a). The likewise inconspicuous male inflorescences produce a cluster of about 25–32 (up to 40 according to Spongberg, 1979) long pink anthers on slender, pendulous filaments (Fig. 4b). The flower number is difficult to determine (see section on floral ontogeny). The opening anthers turn brownish and present co-



FIGURES 1-4. Flowers at anthesis.—1. *Trochodendron aralioides*, nectary stippled.—2. *Tetracentron sinense*.—3. *Euptelea polyandra*.—4. *Cercidiphyllum japonicum*: a, female flower, stigma stippled; b, entire male inflorescence.

pious powdery dry pollen. Nectar is lacking. As in *Euptelea*, anthesis is short in early spring before shoot expansion (March or April at Zürich). The anemophily syndrome is obvious.

PERIANTH

One of the oddities of the Trochodendrales is that the flowers lack a perianth. The only exception is *Tetracentron* with a perianth of four tepals. This was the main reason why *Tetracentron* has been, at times, removed from the other three genera, such as by Harms (1897), who put *Tetracentron* in Magnoliaceae but the other genera in Trochodendraceae.

However, the situation is more complicated. Developmental studies have allowed new insights. For a better understanding of the perianth, an analysis of the entire inflorescence is necessary.

Tetracentron. In morphological terms the inflorescence is a spike (at times with a terminal flower, according to Nast & Bailey, 1945, but not present in my material). Each flower sits in the axil of a subtending bract (= pherophyll in the terminology of Briggs & Johnson, 1979). The four tepals cover the inner floral organs in bud. They are not arranged in a whorl, but in two alternate pairs. The first pair has a transversal position similar to that of the two floral prophylls in many dicots (Fig. 5). In *Tetracentron*, there are no prophylls outside the tepals, but the two outer tepals correspond to prophylls in respect of their position. In correlation with their diminished size—the entire flowers being minute—and thin texture, the tepals often lack well-differentiated vascular bundles (cf. also Nast & Bailey, 1945). An interesting detail are cushions with small, but radially elongated thin-walled epider-

mal cells at the inner base of the tepals (Fig. 6). Presumably they play a role in the opening movement of the tepals.

Trochodendron. The inflorescence is a raceme, usually with a terminal flower ("botryoid" in the terminology of Troll, 1964; see also Briggs & Johnson, 1979). In rich inflorescences the lowermost lateral branch may bear one or more secondary lateral flowers; they are, then, incipient panicles. The lateral flowers of the raceme have two tiny prophylls in a transversal position (Figs. 7–9, 11–13); they are somewhat larger on the lowermost lateral flower (Figs. 14–16). Between the uppermost lateral flower and the terminal flower there are a few scales (Wagner, 1903; Nast & Bailey, 1945; Melville, 1969; Cronquist, 1981) (Fig. 17). They are serially homologous to the subtending bracts (prophylls) of the lateral flowers on the main inflorescence axis. This is a feature that often occurs in botryoids and has nothing to do with a perianth ("Zwischenblätter," Troll, 1964; "metaxyphylls," Briggs & Johnson, 1979). Thus, there are no obvious tepals, as recorded in the literature.

However, in studying young stages of *lateral* flowers, I found very small scales between the two transverse floral prophylls and the androecium (Figs. 9, 10). That they are different from the "metaxyphylls" below the terminal flowers and more intimately connected with the flower is shown by the following features: (1) they are smaller and nearer to the androecium than the metaxyphylls, (2) there is a temporal gap between the early appearing two lateral prophylls (however reduced they are) and the additional scales, and (3) if the scales would correspond to the metaxyphylls one would expect the highest number in the lowermost lateral flower (which has, at times, secondary lateral flowers). In the inflorescence shown in Figures 14–19 the reverse is the case: the lowermost lateral flower (Fig. 18) does not even have a single scale on the abaxial side, whereas an upper lateral flower (Fig. 19) shows a scale.

In the material examined, the number (and apparently also the position) of these scales varies from zero to five. In contrast to the tepals of *Tetracentron*, these scales do not protect the floral organs in any phase of ontogeny. The protective function is provided strictly by the cataphylls and young foliage leaves of the reproductive shoot. In flowers at anthesis these scales are obscured by the general thickening of the floral base (Fig. 7).

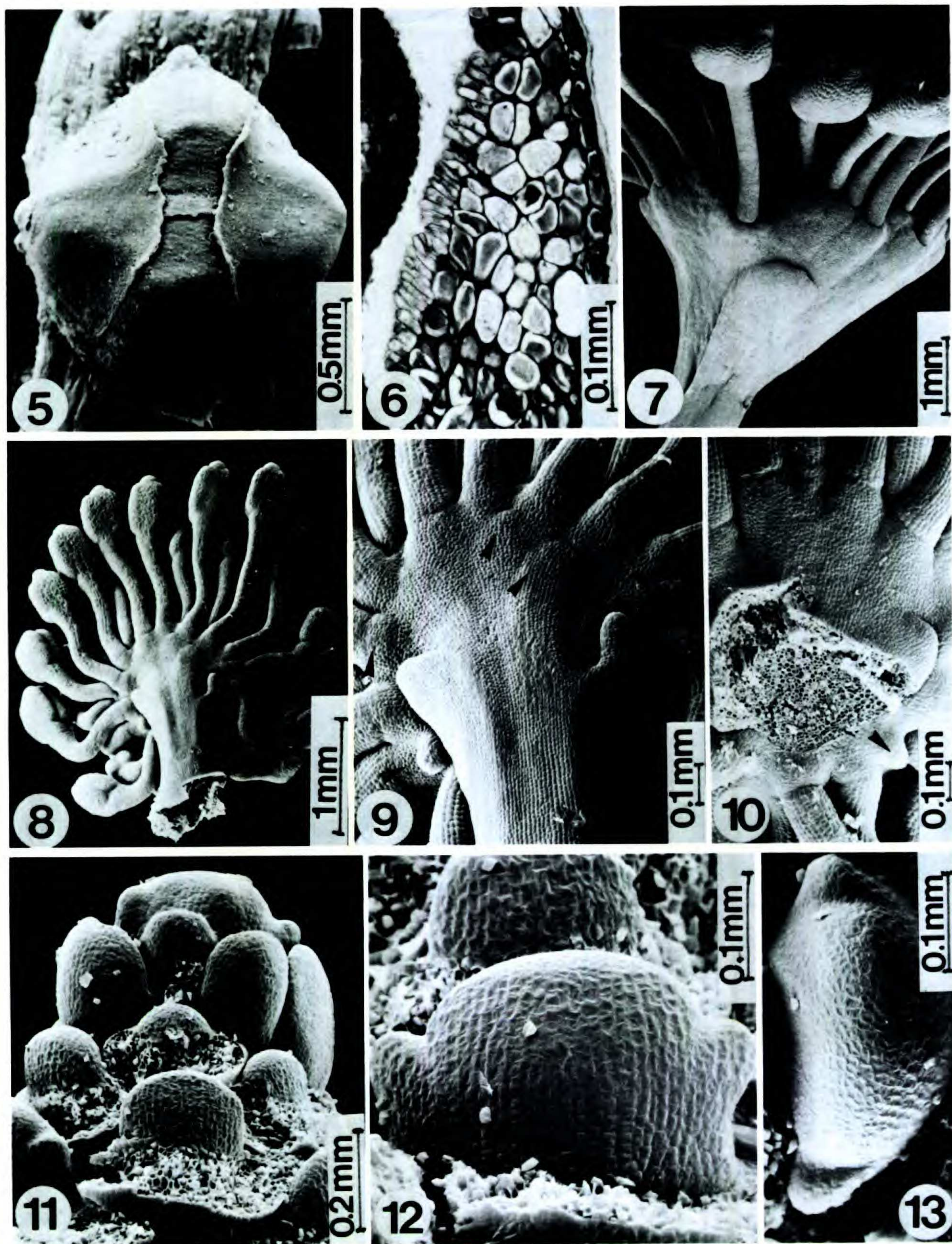
Euptelea. The inflorescences are also racemes, but the main axis of the raceme transforms into a vegetative shoot after production of the reproductive part (proliferation, Troll, 1964; auxotelic raceme, Briggs & Johnson, 1979). The flowers have no perianth (Fig. 22), but the lowermost flowers of a raceme often have one or two tiny transverse prophylls (Endress, 1969) (Figs. 20, 21). After production of the prophylls, the floral primordia of *Euptelea* and *Trochodendron* look similar in their peculiar zygomorphic or bilateral symmetry (see section on floral ontogeny). However, later, the floral axis elongates above the prophylls in *Euptelea* (Fig. 20), but below in *Trochodendron* (Fig. 12). Therefore, at anthesis, the prophylls are at the base of the pedicel in *Euptelea*, but on the top in *Trochodendron*.

Cercidiphyllum. Both perianth and floral prophylls are lacking. The inflorescences are congested spikes (heads).

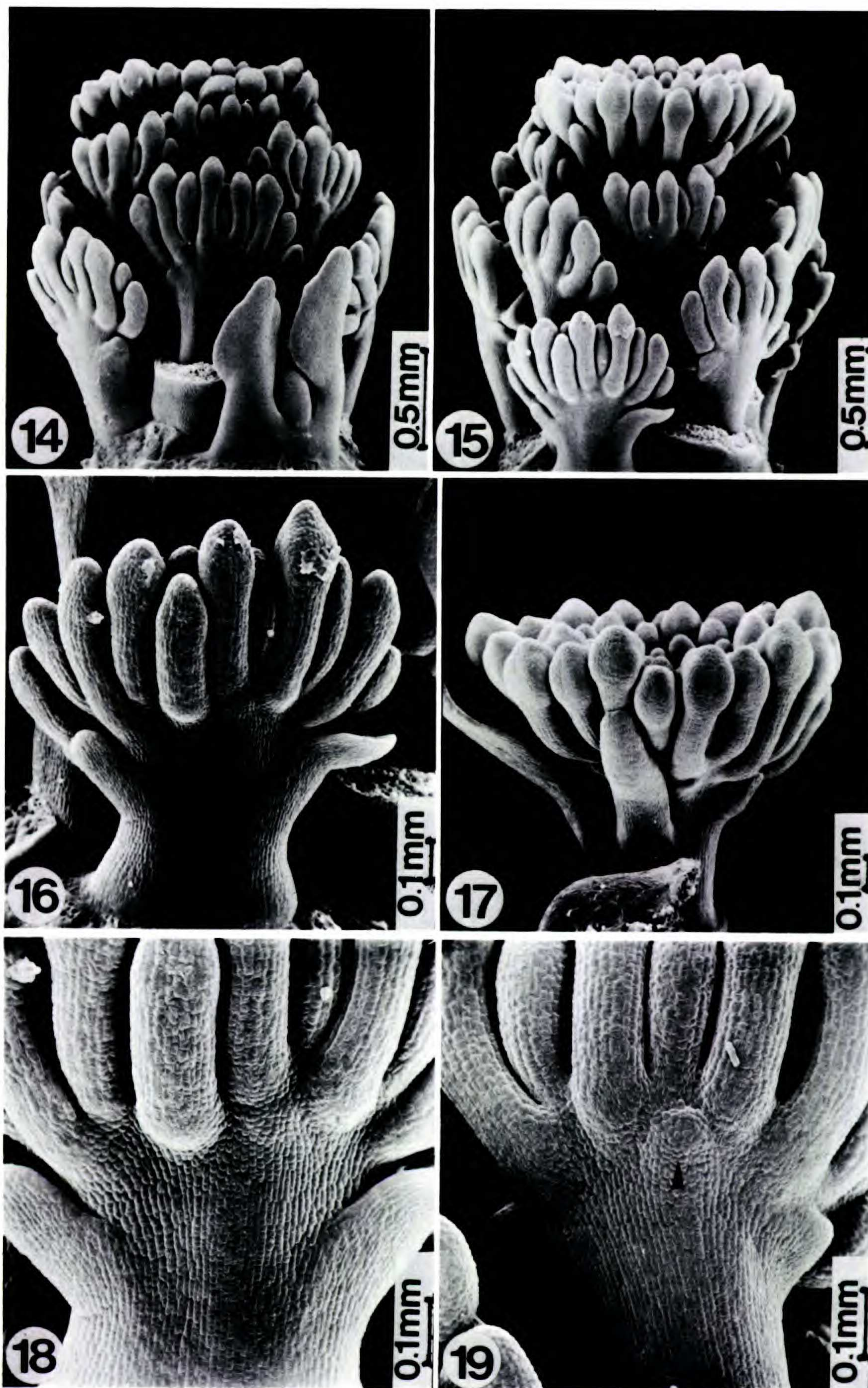
General. How do these new results influence the morphological and phylogenetic interpretation of the perianth in the Trochodendrales? The generally held view is that *Tetracentron* has a perianth of four tepals, but the other genera have naked flowers.

But if we ask instead, "How many phyllomes are between the base of the floral axis and the androecium?" the result is very different. All genera except *Cercidiphyllum* (*Euptelea* at least in some of the flowers) have a first pair of transverse phyllomes that can be called prophylls. *Tetracentron* has two more phyllomes, *Trochodendron* up to five more. In both genera they are small and not or only weakly vascularized (even in *Tetracentron*, see also Nast & Bailey, 1945). Considered this way, there is no sharp contrast between *Tetracentron* and *Trochodendron*. There is rather a gradual reduction from *Tetracentron* to *Trochodendron* and *Euptelea* to *Cercidiphyllum* (Fig. 23).

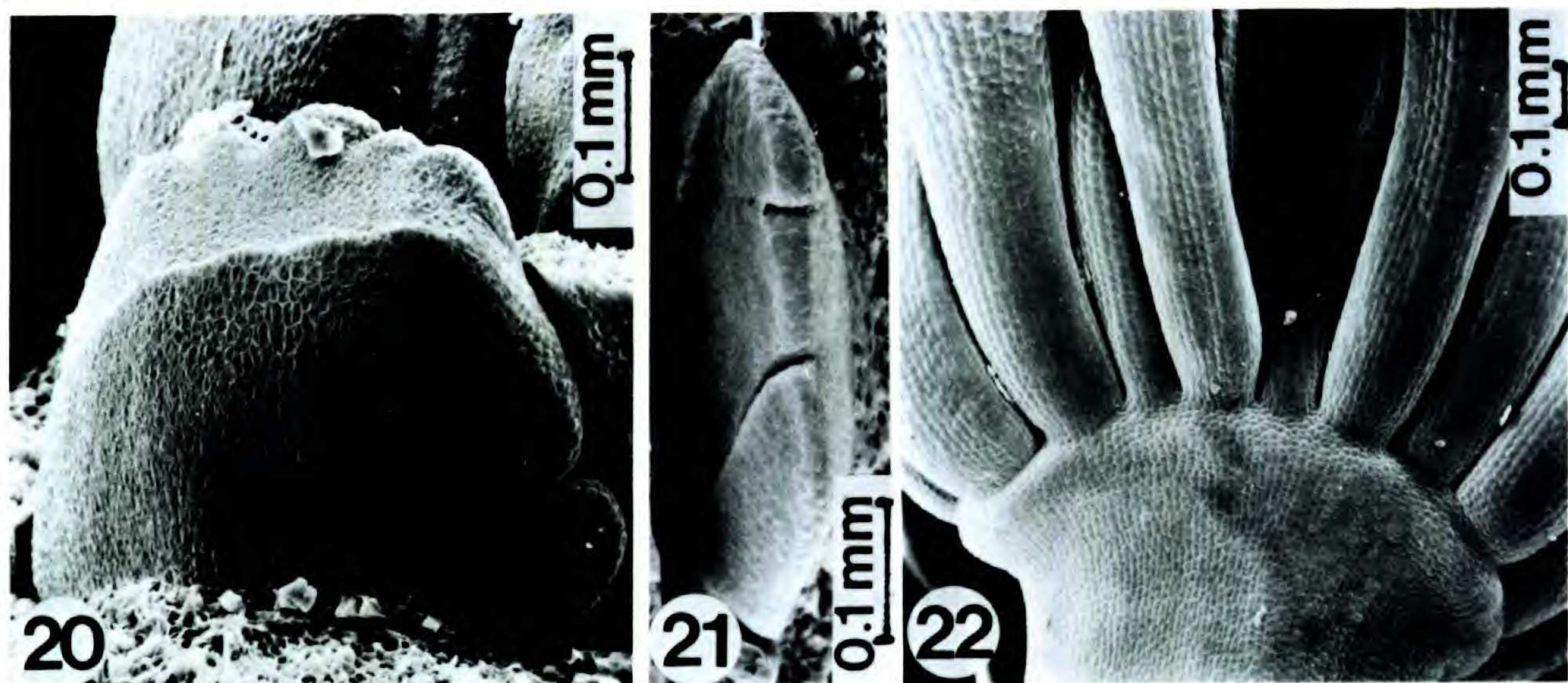
Whether these rudimentary phyllomes in *Trochodendron* should be regarded as tepals or as bracts remains somewhat ambiguous. We can state that there *are* phyllomes between prophylls and stamens, which precede the series of floral organs (sporophylls). At this evolutionary level of flowers exhibiting spiral phyllotaxis and lacking differentiation in calyx and corolla, it is always difficult to delimit a perianth from the preceding series of bracts (e.g., Endress, 1980a, 1980b, for *Austrobaileya* and *Hortonia*; Endress & Sampson, 1983, for Trimeniaceae). However, the long plastochron after formation of the two



FIGURES 5-13. 5, 6. *Tetracentron sinense*.—5. Old flower bud with pherophyll (below) and four tepals, $\times 30$.—6. Base of tepal of flower at anthesis in longitudinal section with small-celled inner epidermis, $\times 140$. 7-13. *Trochodendron aralioides*.—7. Base of flower at anthesis from the side, with one of the two prophylls visible, $\times 10$.—8. Lateral flower from bud (February) from abaxial side, $\times 15$.—9. The same, enlarged, showing the two prophylls and five rudimentary "tepals" (arrows!), $\times 50$.—10. Lateral flower bud with the pedicel removed, showing one rudimentary tepal on adaxial side, $\times 50$.—11. Young inflorescence (July); in lower part floral pherophylls removed to show floral primordia, $\times 65$.—12. Floral primordium from adaxial side, with two (distal) prophylls, $\times 140$.—13. Same, from above, to show the floral zygomorphy, $\times 130$.



FIGURES 14-19. *Trochodendron aralioides*, young inflorescence (August).—14. Entire inflorescence from the side; on right side vegetative bud with two large prophylls, $\times 25$.—15. Same, from the opposite side, $\times 25$.—16. Lowermost lateral flower, with relatively large prophylls, $\times 55$.—17. Terminal flower, after removal of all lateral flowers, to show the “metaxyphylls” (cf. page 300).—18. Same as Fig. 16, enlarged, tepal rudiments lacking, $\times 85$.—19. Lateral flower from middle region, with smaller prophylls and one rudimentary tepal (arrow!), $\times 90$.



FIGURES 20–22. *Euptelea polyandra*.—20. Floral primordium (July) from abaxial side, with one (basal) prophyll, $\times 100$.—21. Younger floral primordium (July) from above, to show the bilateral (or zygomorphic) symmetry, $\times 110$.—22. Base of old floral bud (December), rim around stamens by thickening of floral base, no tepals, $\times 45$.

prophylls may be seen as a sign that the subsequently formed scales are to some extent integrated into the floral organization. In contrast, within the Hamamelidaceae there are obvious reduction series from flowers with well-differentiated protecting sepals in addition to petals (e.g., *Hamamelis*) through flowers with reduced and unprotective tepals (e.g., *Sycopsis*) to perianthless flowers (e.g., *Distyliopsis*) (Endress, 1977, 1978).

I conclude, based on this, that it is highly improbable that the Trochodendrales are primitively completely devoid of a perianth.

ANDROECIUM

Tetracentron and *Trochodendron*. The androecium is composed of four stamens in *Tetracentron*, but of a variable number of 39 to 46 for lateral flowers and around 70 for terminal flowers in *Trochodendron* (Liao, 1973: 34–57). In *Tetracentron* stamens are much smaller and stouter than in *Trochodendron*.

A newly found feature of systematic importance in both *Trochodendron* and *Tetracentron* is that each theca does not open simply by a longitudinal slit but by two valves (Figs. 24–28, 32). The longitudinal dehiscence line extends into two transversal lines at both ends, which results in two window wing-like valves. This feature underlines at the same time the close relationship between *Tetracentron* and *Trochodendron* and their affinities with Hamamelidales (Fig. 32), especially since this feature is otherwise very rare in the angiosperms. Although “valvate” anthers have been mentioned in the literature for various higher groups of the angiosperms, it seems that most taxa actually have simple longitudinal slits without transverse extensions. At present, real valvate anthers seem to be restricted to a few Magnoliidae (Laurales) and Hamamelidae (Fig. 32), whereby those of the Laurales are of a slightly different type. However, the search has to be extended to other angiosperms. Further similarity with Hamamelidales is provided by the ba-

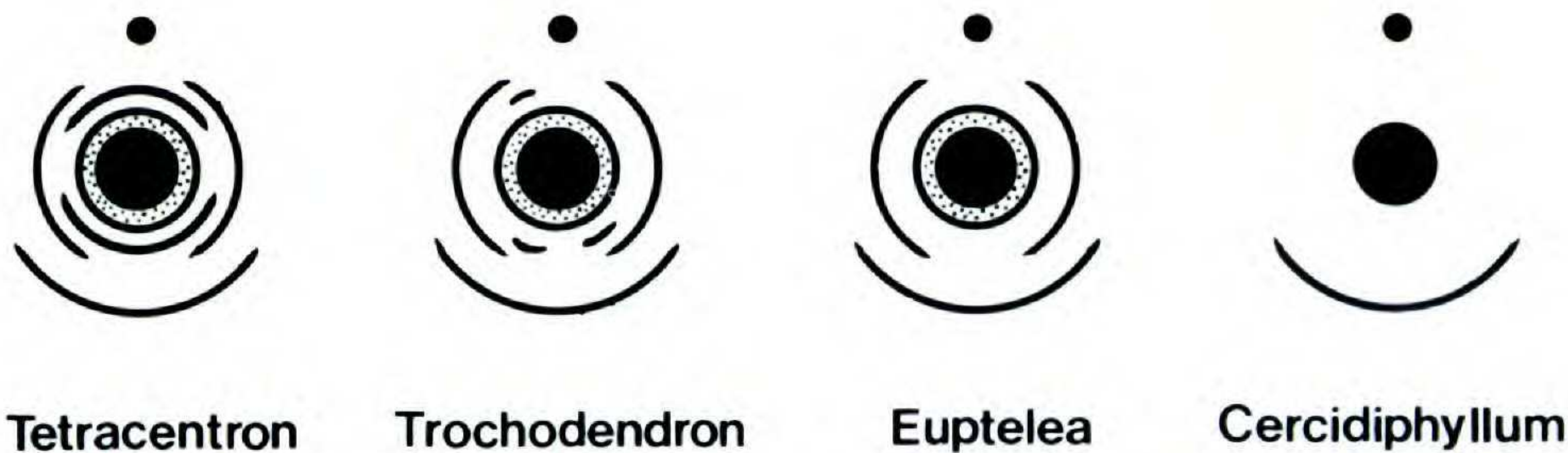
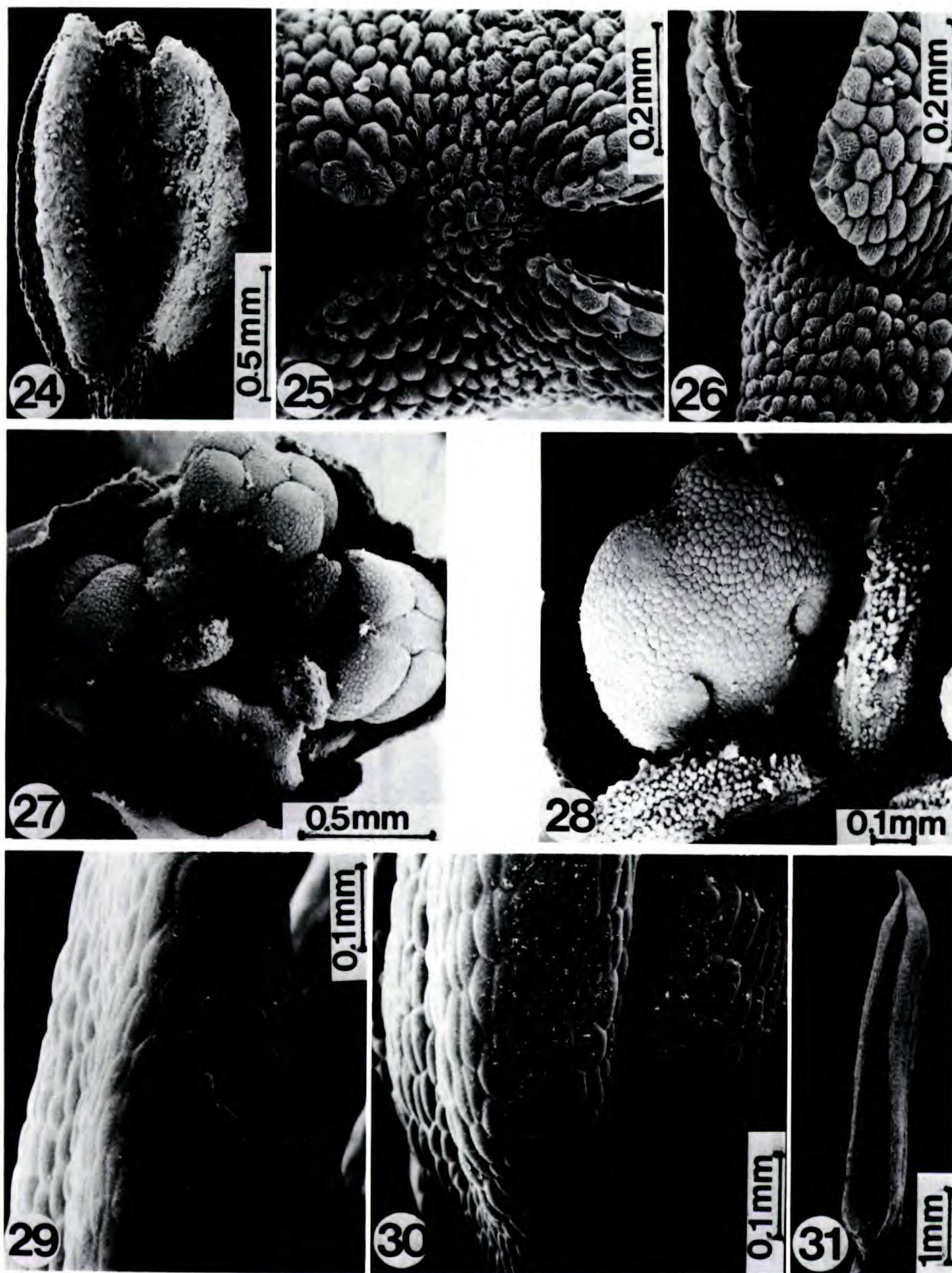


FIGURE 23. Floral diagrams showing floral pherophylls (6:00 position), prophylls (3:00 and 9:00), and tepals. Androecium (stippled) and gynoecium (black) not differentiated. *Cercidiphyllum*: diagram for female flower only.



FIGURES 24-31. 24-26. *Trochodendron aralioides*, mature anthers.—24. From the side, the two valves of a theca, $\times 35$.—25. At opening, from above, connective tip, short lateral extensions of longitudinal slits, $\times 85$.—26. Same anther, lateral extensions on proximal end of slit, $\times 85$. 27, 28. *Tetracentron sinense*, open flower, anthers still closed.—27. Flower from above, showing dehiscence lines of anthers on distal side, $\times 35$.—28. Dehiscence lines on proximal side of anther, from adaxial side, $\times 55$. 29, 30. *Euptelea polyandra*, undeveloped anther, showing dehiscence lines.—29. Distal part, $\times 110$.—30. Proximal part, $\times 110$.—31. *Cercidiphyllum japonicum*, open anther from the side, with simple longitudinal slit, $\times 10$.

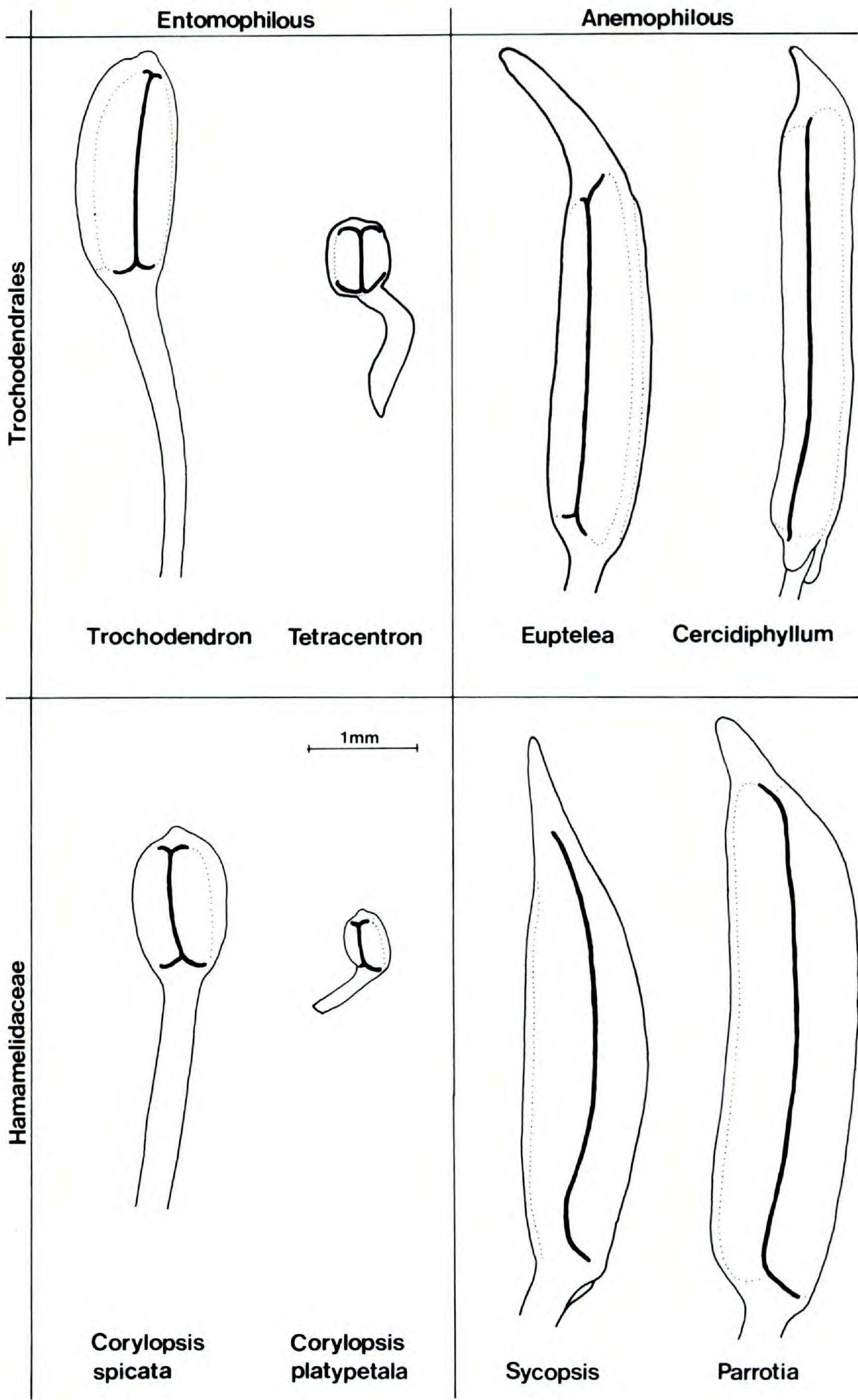


FIGURE 32. Similarity and parallel variation of anther shape, size and dehiscence in correlation with entomo- and anemophily in Trochodendrales and Hamamelidaceae. All stamens from the side, adaxial side left. (*Corylopsis spicata*, *C. platypetala*, *Sycopsis sinensis*, and *Parrotia persica*, all from cultivated material, old Botanical Garden, University of Zürich).

sifixed, more or less latrorse anthers with a rudimentary connective tip (Fig. 32).

Euptelea and Cercidiphyllum. In both genera the stamen number is variable: *Euptelea* with six to 19 per flower (Endress, 1969) and *Cercidiphyllum* with at least seven in the lowermost flowers. As part of the anemophily syndrome, the anthers are long and contain more pollen than in *Tetracentron* and *Trochodendron*. In *Cercidiphyllum* they open by simple longitudinal slits (Figs. 31, 32). However, in *Euptelea*, there are very short horizontal extensions of the dehiscence line, mainly at its lower end, which results in two narrow valves on each theca (Figs. 29, 30, 32). As in *Trochodendron* and *Tetracentron*, the anthers are basifixed, more or less latrorse, and provided with a connective tip. The connective tip, however, is longer in *Euptelea* and *Cercidiphyllum* than in *Trochodendron* and *Tetracentron* (Fig. 32), presumably as a result of the early longitudinal growth of the entire anther.

General. It is striking that the range of anther shape in the four genera of Trochodendrales is repeated in Hamamelidaceae (Fig. 32). Also in Hamamelidaceae, long anthers with mass production of pollen and dehiscence by longitudinal slits occur in predominantly wind-pollinated groups, whereas short anthers with less pollen and dehiscence by valves, on which the sticky pollen is presented, are typical for the mainly insect (often fly!)-pollinated groups (Endress, 1977).

POLLEN

In all four genera the pollen grains are triaperturate and more or less spheroidal, but in *Euptelea* also often pluriaperturate (Pragłowski, 1974; Walker, 1976a, 1976b). The apertures are well delimited and coarsely granulate.

Trochodendron and Tetracentron. In pollen structure the two genera are again strikingly similar, also in details not previously mentioned in the literature. Both are tricolpate. The tectum consists of distinct rods that are irregularly interwoven and form a loose network between the apertures but are crowded into parallel bundles along the aperture borders (Figs. 33, 34, 37). In short, the exine is rugulate-reticulate between the apertures but striate near the apertures in both genera. In both genera, especially in *Tetracentron*, the pollen is very small (10–15 μm diam.). On the whole, the similarity in exine structure between the two genera is even more accentuated

than stated by Pragłowski (1974) and Walker (1976a, 1976b).

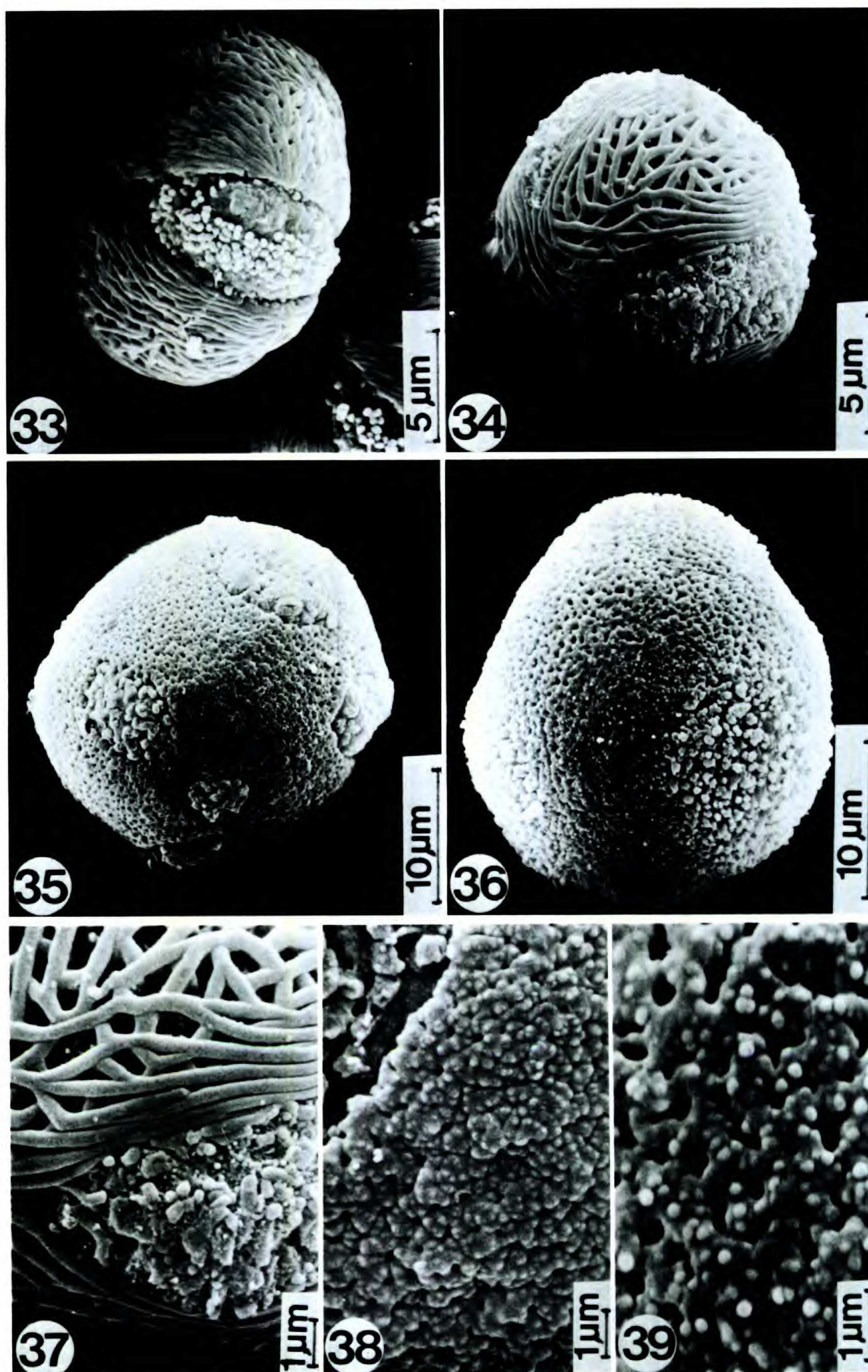
Euptelea and Cercidiphyllum. In both genera the exine is finely reticulate, with minute tectal perforations, and scabrate (with supratectal verrucae). The apertures are shorter, more roundish in outline than in *Trochodendron* and *Tetracentron* (Figs. 35, 36, 38, 39). In both *Euptelea* and *Cercidiphyllum*, the apertural exine is coarsely structured. *Euptelea* pollen often has more than three apertures, in contrast to *Cercidiphyllum*. In both genera the pollen is considerably larger (20–30 μm diam.) than in *Trochodendron* and *Tetracentron* and fits in the normal range of wind-dispersed pollen (cf. Whitehead, 1969).

Again, the parallel between the pollen of *Euptelea* and *Cercidiphyllum* and the anemophilous genera of the Hamamelidaceae is striking in the trend to shorter apertures and more than three apertures, finer reticulation of the extra-apertural exine, and supratectal verrucae (Endress, 1977; Bogle & Philbrick, 1980).

GYNOECIUM AND NECTARY

Trochodendron. Leinfellner (1969b) gave a brief survey of the gynoecial morphology of Magnoliales, Laurales, and Trochodendrales. The elaborate diagram of a gynoecium of *Trochodendron* in Nast and Bailey (1945) does not show all the basic gross morphological features. The extension of the inner and outer surface in some critical regions remains unclear.

In *Trochodendron* the carpel number of the gynoecium varies around eight in lateral flowers and around ten in terminal flowers. Smith (1945) found a range of (4)6–11, Liao (1973) a range of 7–11, and Cronquist (1981) a range of 4–11 (–17). In the styler region the carpels are free and slightly recurved (Figs. 1, 40, 41a–c, 45). In the ovary, the carpel flanks are congenitally fused (Fig. 41e–i). Above the ovary there is a short zone where the neighboring, contiguous carpels are postgenitally fused (Fig. 41d). The ovary is partially inferior (Fig. 40). In the upper part of the ovary a compitum is formed by postgenital fusion of the carpels in the center, while in the lower portion of the ovary the carpels do not meet in the center, but form a ring around a central hole (Figs. 40, 41e–g). The compitum, however, is rather diffuse, because the ventral slits that are lined with a pollen tube transmitting epidermis are very long in horizontal extension.



FIGURES 33–39. 33–36. Pollen grains.—33. *Trochodendron aralioides*, $\times 2,700$.—34. *Tetracentron sinense*, $\times 3,000$.—35. *Euptelea polyandra*, $\times 1,700$.—36. *Cercidiphyllum japonicum*, $\times 2,000$. 37–39. Details of pollen surface.—37. *Tetracentron sinense*, same as Fig. 34, $\times 6,000$.—38. *Euptelea polyandra*, $\times 6,000$.—39. *Cercidiphyllum japonicum*, $\times 9,000$.

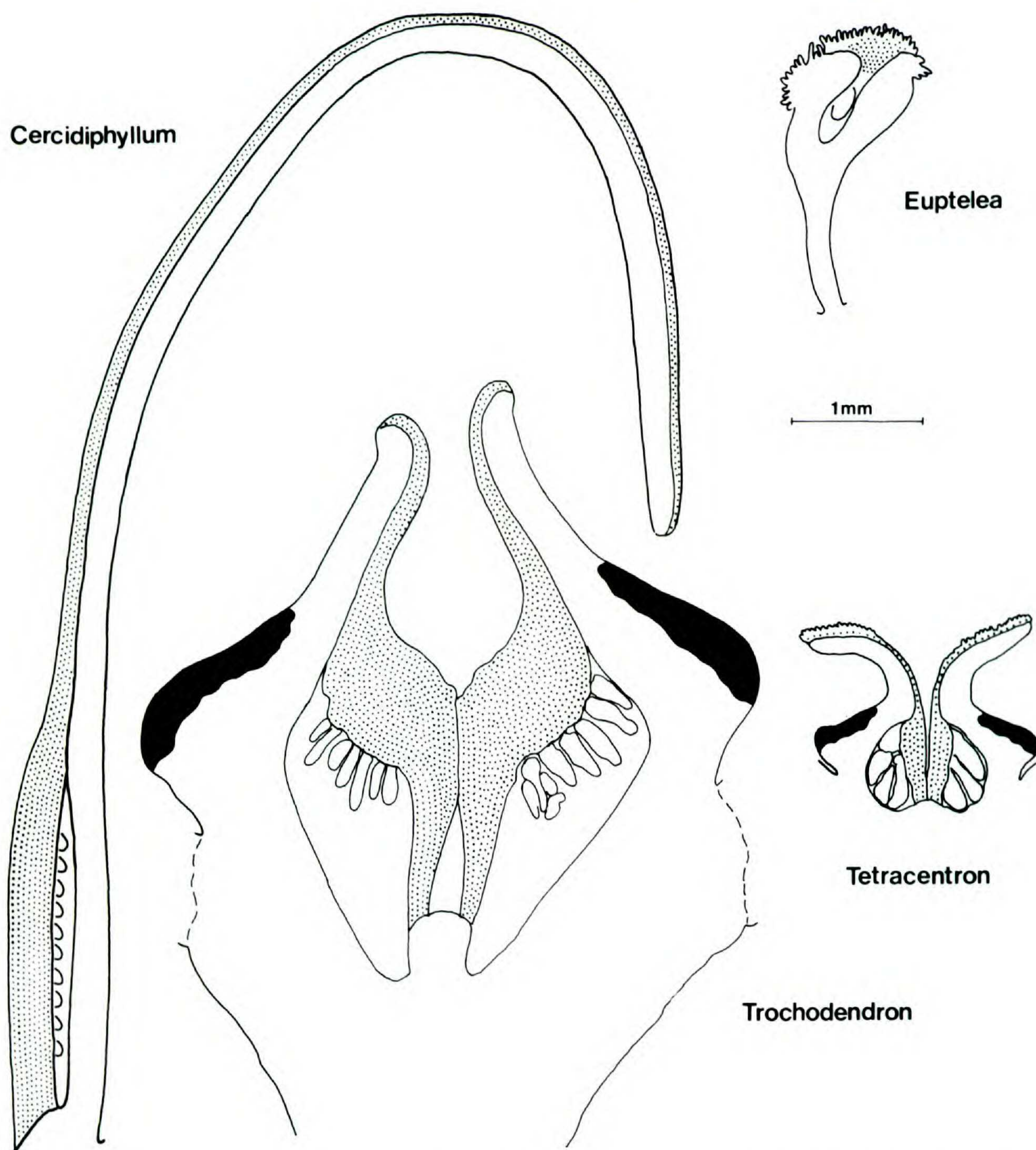


FIGURE 40. Median longitudinal sections of carpels, with ventral side on the left (*Cercidiphyllum*, *Euptelea*), and gynoecia (*Trochodendron*, *Tetracentron*) at anthesis, with outer and inner morphological surfaces (stippled, region of postgenital fusion; black, nectariferous region).

The compitum is, therefore, not as elaborated as the centralized types in the higher advanced angiosperm groups (Carr & Carr, 1961). Again, the similarity with the Hamamelidaceae is obvious (cf. Endress, 1967).

The stigmatic epidermis differentiates unicellular papillae of a dry type (category DPU in the classification of Heslop-Harrison, 1981) (Fig. 46).

Ontogenetically, the hole in the center of the gynoecium base arises because the fairly high number of carpels is arranged more or less in a whorl and therefore leaves a free field in the center of the floral apex. Gynoecial development is

slow and retarded compared with that of the androecium. In mid-September, when the outer stamens were morphologically already well differentiated, the carpels were still shallow, hippocrepiform mounds (Figs. 56, 57). In mid-February, the postgenital fusion within and between the carpels had not yet started.

The carpels have a conspicuous dorsal bulge. This bulge is differentiated as a nectary (see Tieghem, 1900!) (Figs. 1, 40, 45, 50) and is vascularized by numerous phloic strands that are connected with the dorsal carpellary bundles (Nast & Bailey, 1945; Pervukhina, 1962) (Fig.

41d, e). It forms an open landing platform exposed to visitors. The epidermis of the nectary is covered with numerous slightly sunken stomata. Each stoma is surrounded by a ring of several epidermal cells with conspicuous cuticular folds (Figs. 52, 54).

All or part of the 15–30 ovules (15–20, my data; 15–28, Liao, 1973; 25–30, Cronquist, 1981) in each carpel develop into many small dust-like seeds, suited for wind-dispersal. They are released from capsules that open by ventral and short dorsal slits. The mature ovules have long integuments and a chalazal protrusion, which both contribute to seed appendages. In the chalazal appendage the ovular vascular bundle forms a hair-pin loop (Nast & Bailey, 1945; Mohana Rao, 1983). The testa differentiates five cell layers, the middle layer being sclerified (Melikian, 1973).

Tetracentron. The gynoecium of *Tetracentron* although strikingly similar to that of *Trochodendron* (Fig. 40), differs in that it is much smaller and contains only four carpels (Figs. 42c, 51), each with five or six ovules. The very similar differentiation of a nectary should be especially emphasized, since it has not been reported previously, although its presence was mentioned by Cronquist (1981). The numerous stomata on the dorsal carpellary bulges are also slightly sunken below the general surface (by the smaller size of the guard cells compared with the other epidermis cells) and surrounded by a ring of epidermal cells with prominent cuticular folds (Figs. 53, 55). Striking are also the facts that in both genera the stigma is presumably dry and has unicellular papillae (Fig. 47), that the ovary is syncarpous and semi-inferior (Fig. 40), that the ovary locules are filled with copious secretion around the ovules, and that dust-like seeds (testa five-layered with middle layer sclerified, Melikian, 1973) with a chalazal and micropylar appendage are released from small capsules. The ovules with the long integuments and chalazal protrusion with a hair-pin-like vascular bundle are very similar (Nast & Bailey, 1945) in *Tetracentron* and *Trochodendron*. Also in both genera the carpels have five main vascular bundles, three dorsal ones and one lateral one on each side (Fig. 42). *Trochodendron* has more secondary lateral veins appropriate to its larger size. In *Tetracentron* the nectary does not have a separate vascular supply, probably due to the much smaller size of the gynoecium (Fig. 42b, c).

Cercidiphyllum. The female flower consists

of nothing more than a slightly stipitate single carpel on a rudimentary floral axis (Fig. 4a) (Solereder, 1899). The carpel is plicate throughout (in the terminology of Leinfellner, 1950) without any ascidiate basal portion (Fig. 43). Leinfellner's (1969b) observation of a slight indication of an ascidiate base in *Cercidiphyllum* could not be confirmed with my material (Fig. 43k). The ovary contains about 17–24 lateral ovules in two rows (17–20, my data; 20–24, Harms, 1916). The ovary is relatively small at the time of pollination and the ovules immature, and the stigma occupies about a third of the length of the carpel (Fig. 4a); it is extended over almost the entire circumference of the carpel apically and tapers towards the base (Figs. 4a, 43a, b). The stigmatic surface bears unicellular papillae and is of a dry type (Fig. 49). The carpel has three main vascular bundles (Fig. 43), a median and two laterals with a network of secondary lateral bundles in between, which are only weakly differentiated at anthesis.

The seeds have a conspicuous micropylar and a chalazal appendage with a vascular bundle describing a hair-pin loop. However, the integuments protrude less over the micropyle than in *Trochodendron* and *Tetracentron* (Swamy & Bailey, 1949).

Euptelea. The gynoecium consists of about eight to 31 free carpels (Smith, 1946; Leinfellner, 1969a; Endress, 1969). The carpels are conspicuously stipitate, but lack a style. The ovary is strongly ascidiate (Fig. 44) and contains 1–3(–4) lateral ovules that are, as in *Cercidiphyllum*, immature at anthesis. The stigmatic surface sits immediately on the ovary; it bears long, unicellular papillae and is of a dry type (Fig. 48). In the carpel three vascular bundles differentiate (Fig. 44), a (dorsal) median and two laterals. The two laterals fuse in the ascidiate region in proximal direction and the resulting ventral median bundle fuses with the dorsal median in the stipe (Fig. 44; Leinfellner 1969a). The carpel shape of *Euptelea* is very distinctive and resembles certain Magnoliidae, such as Winteraceae, Schisandraceae, and Ranunculaceae, much more than any Hamamelidae.

FLORAL ONTOGENY, PHYLOTAXIS, AND FLORAL SYMMETRY

Floral symmetry and phyllotaxis are intimately correlated, at least in early developmental stages. Examples were recently shown by Tucker (1984). It seems that there is also a connection between the early floral symmetry and the ar-

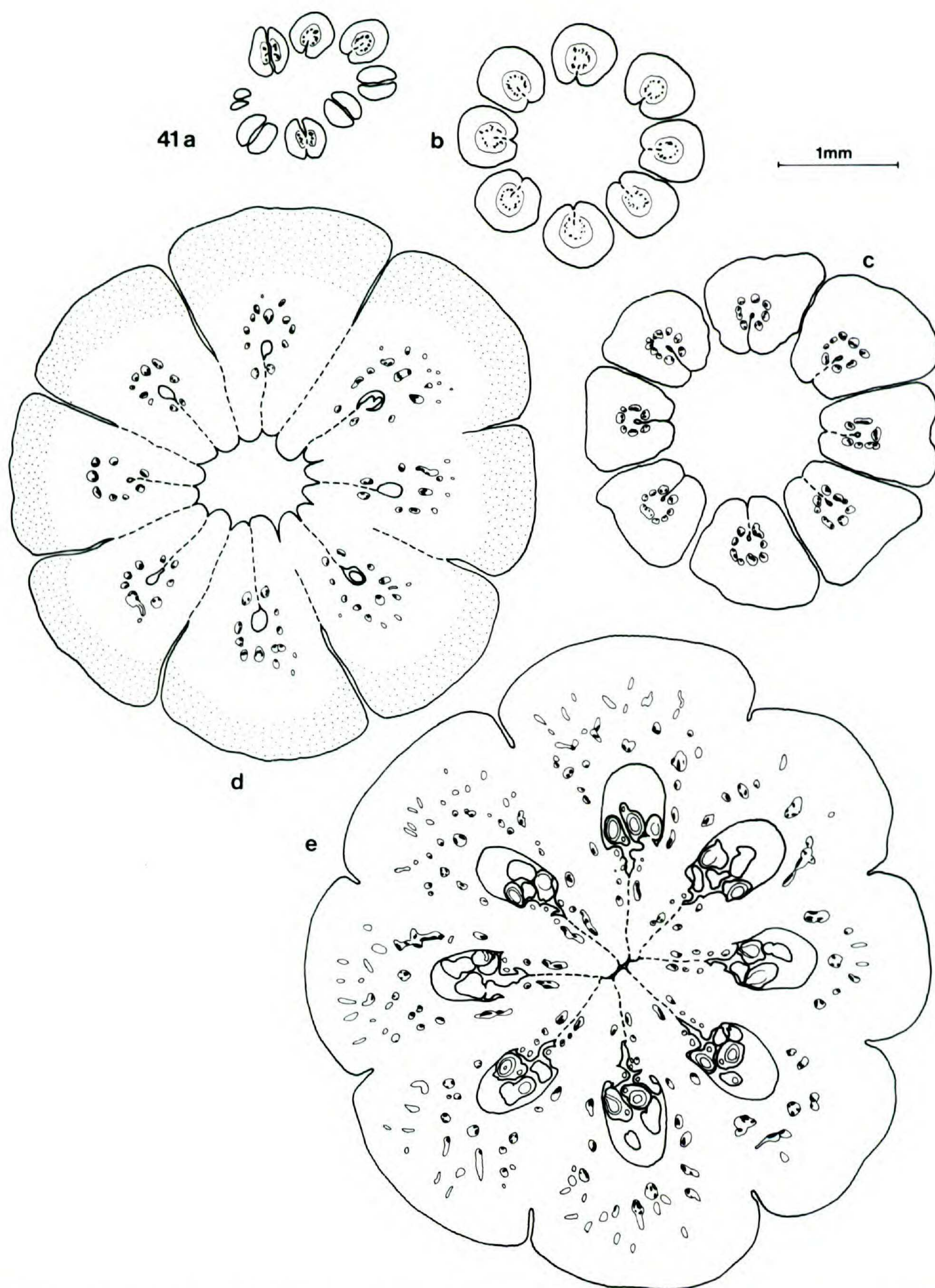
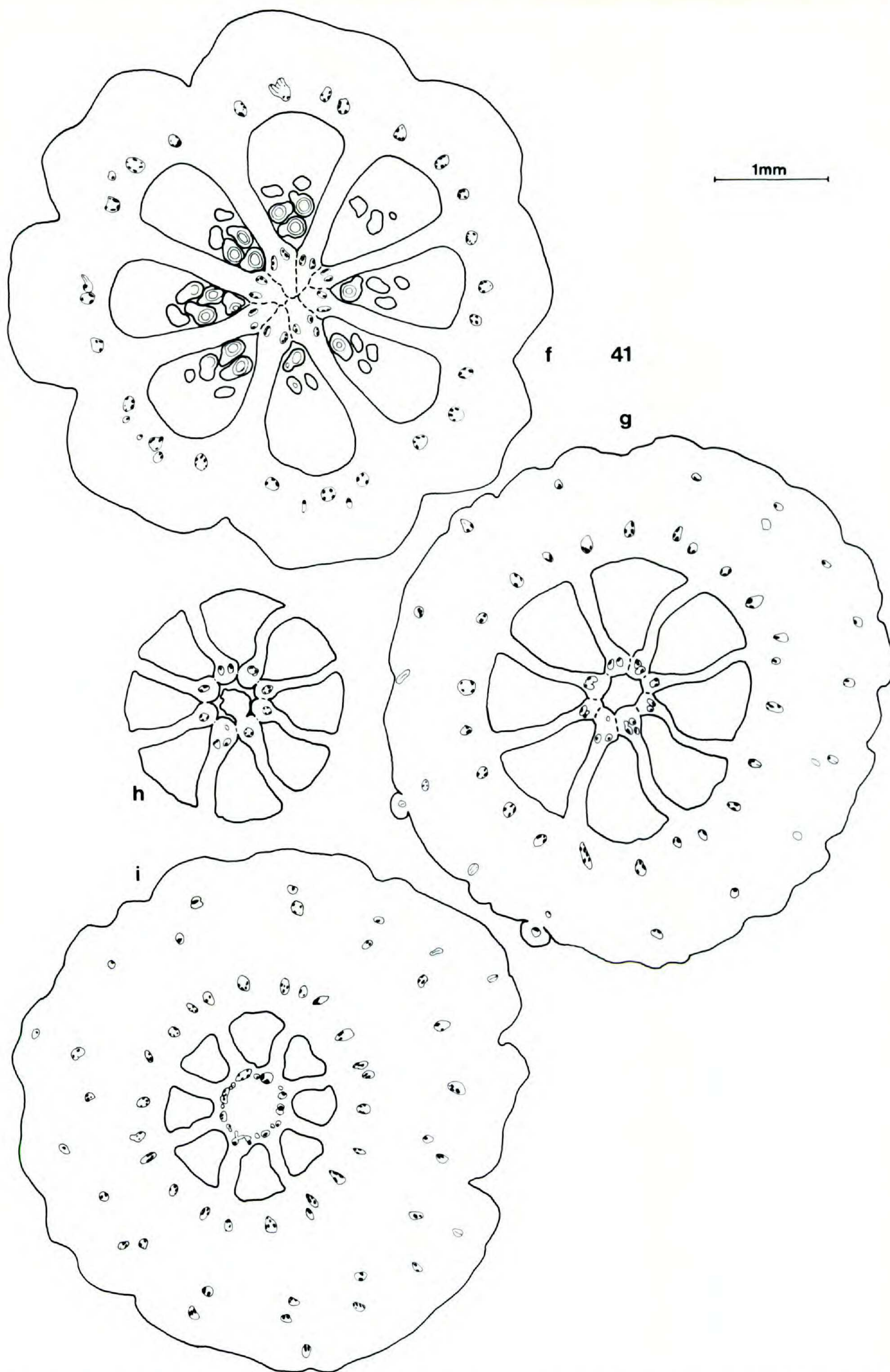
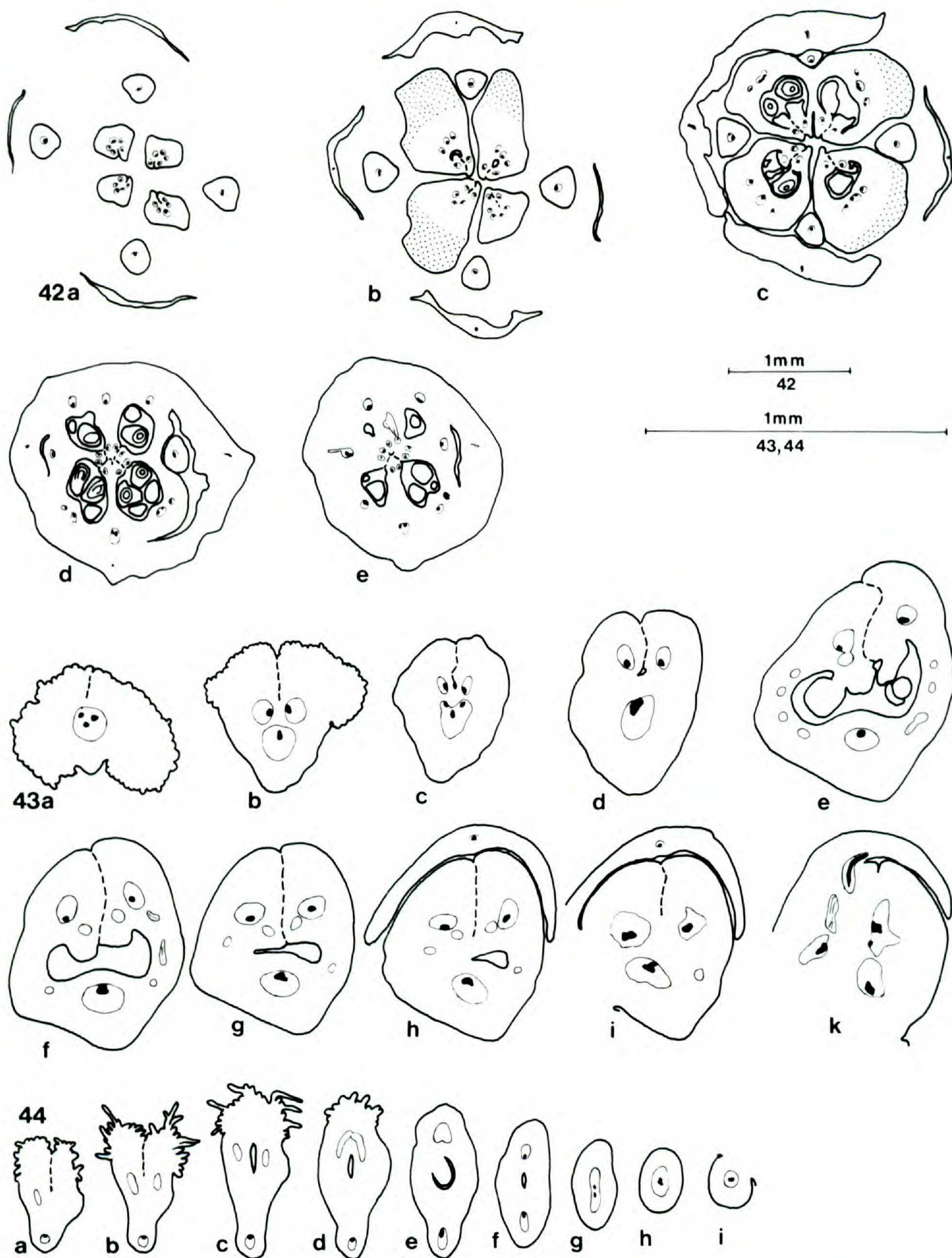


FIGURE 41a-e. *Trochodendron aralioides*. Series of transverse sections of gynoecium at anthesis (dashed lines, regions of postgenital fusion; black, xylem in vascular bundles).—a. Stigmatic region.—b. Upper styler region.—c. Lower styler region.—d. Transition region between style and ovary (stippled, nectariferous tissue).—e. Upper symplicate region of ovary where the carpellary flanks meet in the center; note numerous peripheral phloic bundles supplying nectaries.

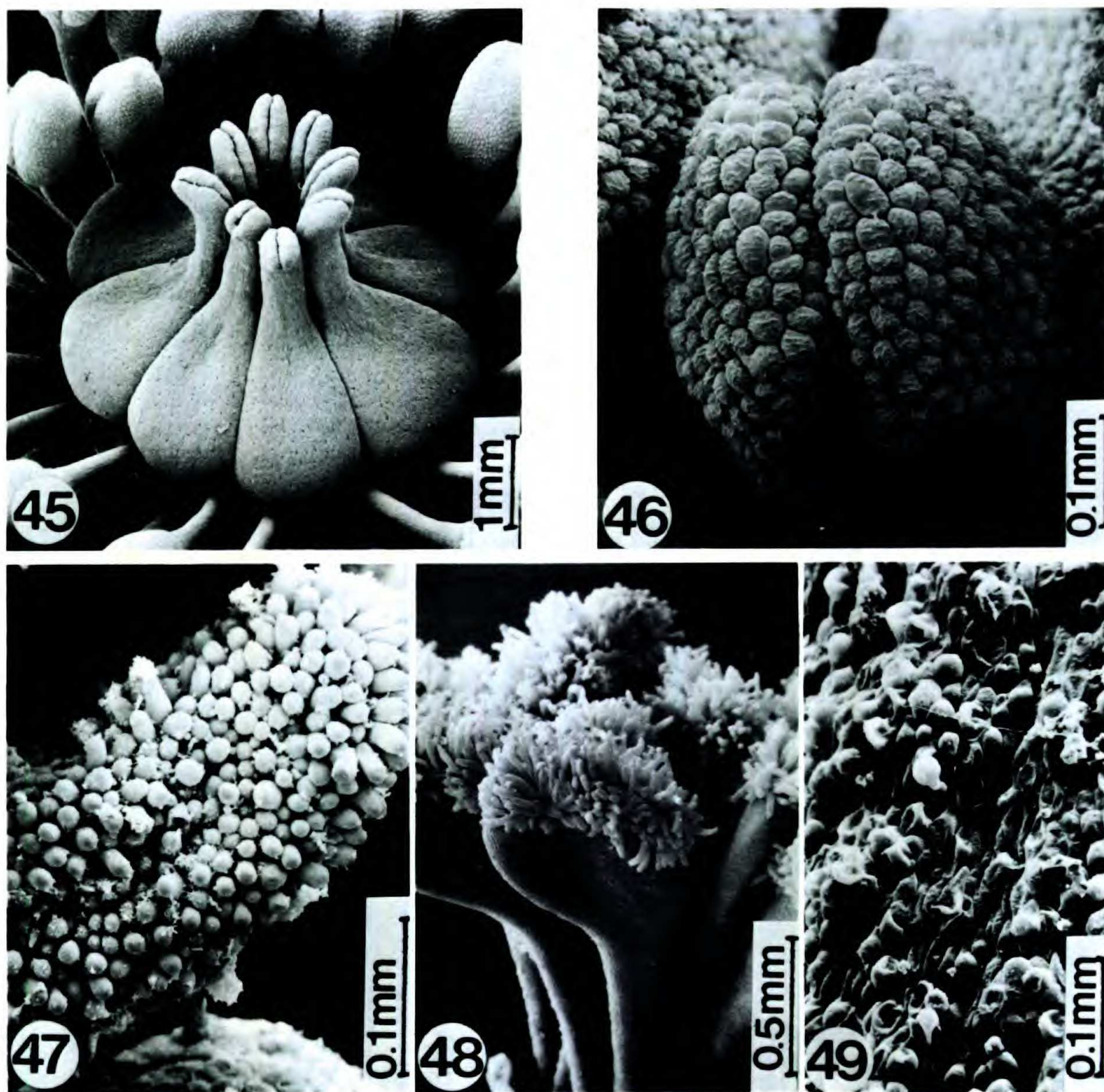
FIGURE 41f-i. *Trochodendron aralioides*. Series of transverse sections of gynoecium at anthesis (dashed lines, regions of postgenital fusion; black, xylem in vascular bundles).—f. Middle symplicate region of ovary with



minimal extension of postgenitally fused region of carpellary flanks meeting in the center (compitum).—g. Lower symplicate region of ovary with carpellary flanks retracted from the center, leaving a hole; at the periphery stamen bases and stamen traces appear.—h. Transition region between symplicate and synascidiate region (only center of ovary drawn).—i. Synascidiate region of ovary.



FIGURES 42–44. Transverse sections of a flower (*Tetracentron*, *Cercidiphyllum*) or of a carpel (*Euptelea*) at anthesis (dashed lines, regions of postgenital fusion; black, xylem in vascular bundles).—42. *Tetracentron sinense*, abaxial side below (stippled, nectariferous regions): a, stylar region; b, transition region between styles and ovary; c, transition region between apocarpous and symplicate region; d, symplicate region, the two median stamens fused with floral base, the two lateral stamens (partially) free; e, transition region between symplicate and synascidiate region.—43. *Cercidiphyllum japonicum*, floral pherophyll and ventral side of carpel facing upwards (in h–k): a, b, upper (a) and lower (b) stigmatic regions (wavy outline, receptive surface); c, middle stylar region; d, transition region between style and ovary; e, ovary; f, ovary below placental region; g, ovary base; h, transition region between ovary and carpellary base; i, massive carpellary base, ventral slit (by dashed line) still present; k, carpellary base united with floral pherophyll on left side, lowermost extension of ventral slit still present.—44. *Euptelea polyandra*, ventral side of carpel facing upwards: a, b, plicate apex of carpel; c, upper ascidiate part of carpel; d, lower end of stigma, lateral bundles fusing into ventral median bundle; e, ovary with lateral ovule; f, lower end of ovary locule; g, h, carpellary base, ventral and dorsal median bundle fusing; i, carpellary base partially united with floral base.



FIGURES 45–49.—45. *Trochodendron aralioides*. Gynoecium at early anthesis, $\times 10$. 46–49. Stigmatic surfaces at anthesis.—46. *Trochodendron aralioides*, $\times 120$.—47. *Tetracentron sinense*, $\times 170$.—48. *Euptelea polyandra*, $\times 30$.—49. *Cercidiphyllum japonicum*, $\times 130$.

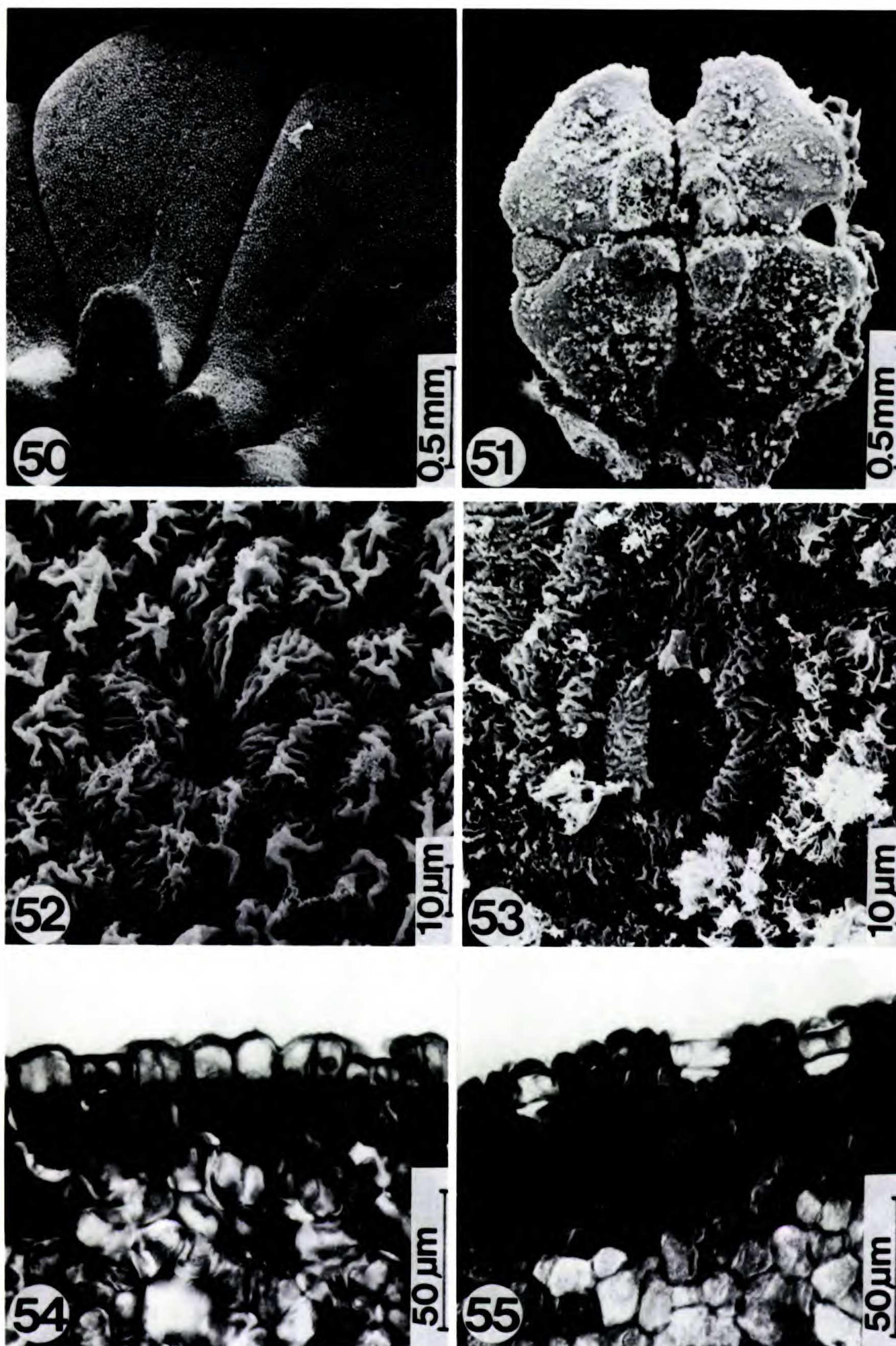
chitecture of the entire shoot bud (Endress, 1969), which is obvious in *Trochodendron*, *Euptelea*, and *Cercidiphyllum*.

Trochodendron. The young flowers have been shown to pass through a zygomorphic phase with a conspicuous *adaxial* growth retardation of stamen primordia, although at anthesis they have (re)gained a radial symmetry (Pervukhina & Yoffe, 1962). However, this is only true for the lateral flowers of the inflorescence (Fig. 56), and the terminal flower is radial throughout its ontogeny (Fig. 57).

The androecium has usually been described as being spirally arranged. This seems to be true from the earliest ontogenetic stages and it can be extended to the gynoecium. This is even implied by the frequent occurrence of eight carpels, which is a Fibonacci number. As in *Illicium* (Robertson & Tucker, 1979), the broad residual floral apex

favors a secondary more or less whorl-like arrangement of the spiral carpels. It is interesting that the spiral arrangement is also present in the lateral flowers. Therefore, it can be supposed that in the youngest stages when the stamens and carpels are initiated, the floral apex is (at least) not (strongly) zygomorphic. This problem and the exact phyllotaxis have to be studied by detailed ontogenetic investigations.

Tetracentron. The flower is described as having three tetramerous whorls, with the stamens opposite the tepals, but the carpels alternating with the stamens (Bailey & Nast, 1945). However, the flowers are more exactly described as dimerous in the perianth and androecium with four alternate pairs of organs, but tetramerous in the gynoecium (Fig. 2). The two tepal pairs are distinct by their aestivation, the two stamen pairs by the position of the anthers. Only the two me-



FIGURES 50–55. 50, 51. Gynoecium at anthesis, from above, showing nectariferous dorsal bulges of the carpels.—50. *Trochodendron aralioides*, sunken stomata visible as black dots, $\times 25$.—51. *Tetracentron sinense*, styles removed, nectaries covered with secretion, $\times 30$. 52, 53. Sunken stoma of nectary, encircled by several epidermal cells.—52. *Trochodendron aralioides*, $\times 600$.—53. *Tetracentron sinense*, $\times 960$. 54, 55. Longitudinal section of nectariferous surface with sunken stomata.—54. *Trochodendron aralioides*, $\times 350$.—55. *Tetracentron sinense*, $\times 350$.

dian stamens are contiguous in bud, while the two lateral ones are more remote. Further, the lateral tepals and stamens are attached at a lower level than the median ones, as seen from trans-

verse section series (Fig. 42d). Therefore, the flowers are not exactly radial, but slightly bilaterally symmetric. Unfortunately, the early floral ontogeny is still unknown in *Tetracentron*.

Euptelea. The flower has a radial symmetry at first glance. However, the floral base is broader in transverse than in median direction, and is, therefore, bilaterally symmetric as in *Tetracentron*. Interestingly, floral primordia show a similar pattern of zygomorphy as in *Trochodendron*. However, it is just reversed in that mostly the abaxial side is retarded (Figs. 58, 59).

Cercidiphyllum. The female flowers are necessarily "zygomorphic," since they consist of a single carpel, which is directed towards the subtending bract (pherothyll of the flower). Leroy (1980) ascribed a special morphological significance to this position. However, it is the position that would be expected for the first phyllome of a lateral shoot with an adaxial prophyll in the same way as it occurs in the vegetative region of *Cercidiphyllum*. Ontogeny shows that not only the flowers but also the entire inflorescence is zygomorphic (Fig. 60). The inflorescence primordium is directed towards the adaxial side. The flowers appear in one or two decussate pairs. The first (transversal) pair of subtending bracts (pherothylls of the flowers) is not exactly opposite, but both are positioned somewhat towards the adaxial side. The second (median) pair of pherothylls is exactly opposite, since it is situated in the symmetry plane of the inflorescence (Fig. 60). One or both pherothylls of the second pair may be lacking, but its "carpel" is present (Fig. 61). Other authors have found up to three (to four) pairs of flowers (Swamy & Bailey, 1949; Spongberg, 1979). Van Heel (pers. comm.) observed a distinct rudimentary floral apex between the carpel and the pherothyll in another specimen.

The male flowers of *Cercidiphyllum* are difficult to delimit. The inflorescence contains about 25–32 stamens (Harms, 1916: 16–35) (Figs. 68, 69). Since the symmetry of the young inflorescence and the position of the bracts in the floral region is the same as for the female, a similar position for the flowers has to be expected: two more or less opposite flowers or several flowers in decussate pairs (Figs. 62–67). However, it is difficult to find floral boundaries. All stamens have the thecae in a lateral position relative to the inflorescence axis and all have collateral bundles or at least the xylem more towards the center of the inflorescence axis (Figs. 68, 69). From this one can judge that all turn their ventral side towards the inflorescence axis. According to this interpretation of the inflorescence, all flowers would, then, be highly zygomorphic, with sta-

mens only on the abaxial side of the flower. In early ontogeny the median stamen of each flower would be the largest, the lateral ones successively retarded (Figs. 62, 65, 67). Thereby, the lowermost flower on the adaxial side of the inflorescence axis (frontal view in Fig. 65) would contain the highest stamen number, whereas the lowermost flower on the abaxial side (frontal view in Fig. 64), the lowermost lateral flowers (frontal view in Figs. 66, 67), and the more apical flowers of the inflorescence would contain fewer stamens.

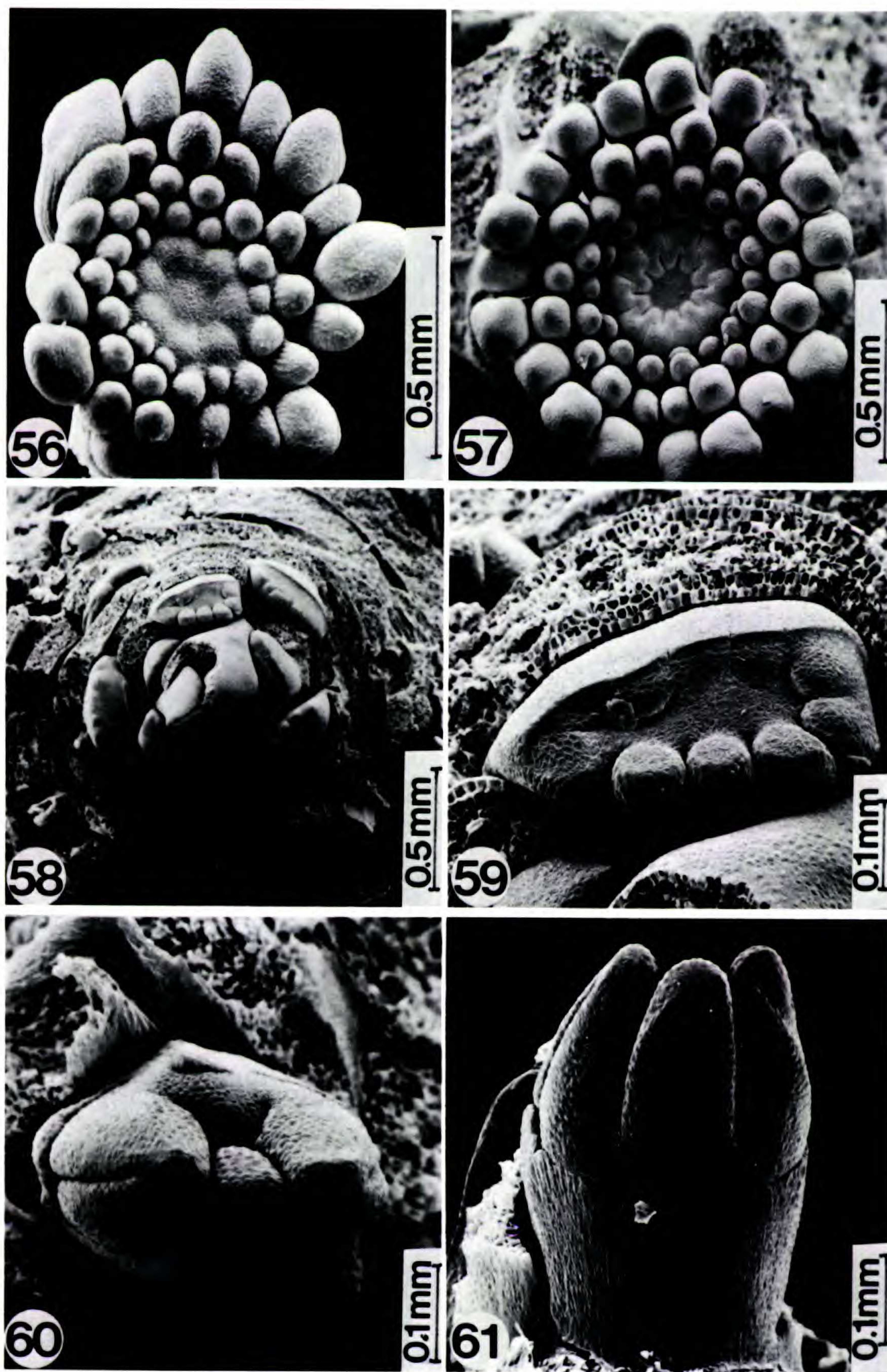
Another tentative, but perhaps less convincing, interpretation would be that the first pair of individual flowers consists of the row of about seven stamens adjoining each of the two lateral bracts. Each bract of the second (i.e., the median) pair (if present at all) has only about one to three stamens in its axil. The following stamens replace bracts in some sense and form a terminal flower (as in some Hamamelidaceae, cf. Endress, 1978; Wisniewski & Bogle, 1982). The residual apex on top of the inflorescence would be the apex of the inflorescence in the first interpretation, but the apex of the terminal flower in the second (Fig. 68a). More information could be expected if the search is extended to other specimens. Swamy and Bailey (1949) depicted a male inflorescence that is easier to interpret since groups of several stamens are situated in the axils of two successive pairs of bracts. Here all flowers seem to consist of eight to 13 stamens.

SOME HISTOLOGICAL FLORAL FEATURES OF SYSTEMATIC INTEREST

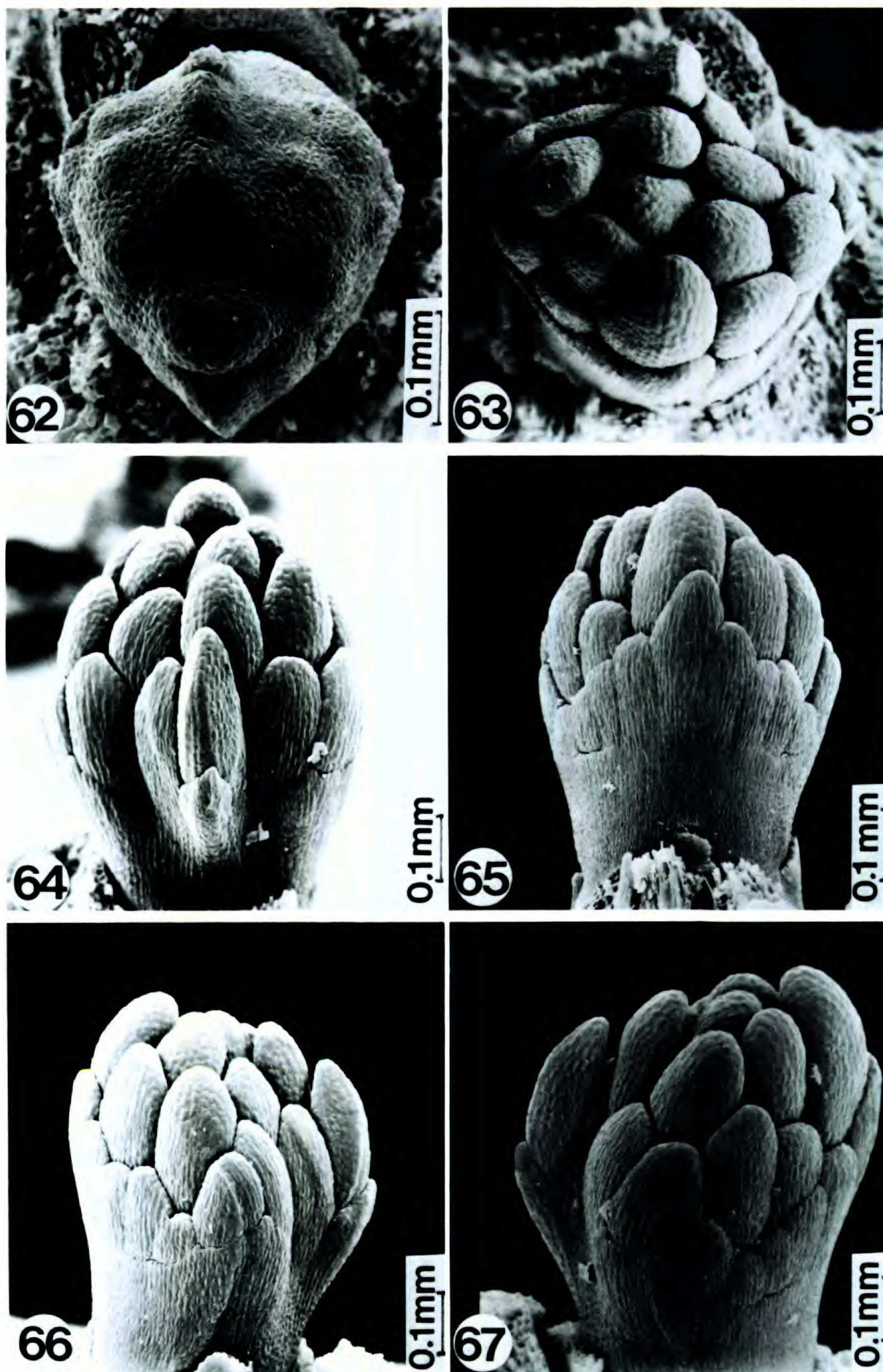
In *Tetracentron* all floral organs contain scattered enlarged cells with the contents dissolved in the fixed and sectioned material (Fig. 70). They much resemble the so-called "oil" cells that are generally present in many Magnoliidae, but absent in Hamamelidae. They are often more or less spherical as in Magnoliidae, apparently in contrast to the vegetative region where they have been described as elongate or branching by Bailey and Nast (1945), or termed "Sekretschläuche" by Harms (1897).

In *Trochodendron* similar cells differentiate into sclerified, branched idioblasts. However, in the gynoeceum, at least at anthesis, many of these cells are not sclerified and presumably also correspond to "oil" cells (Fig. 71).

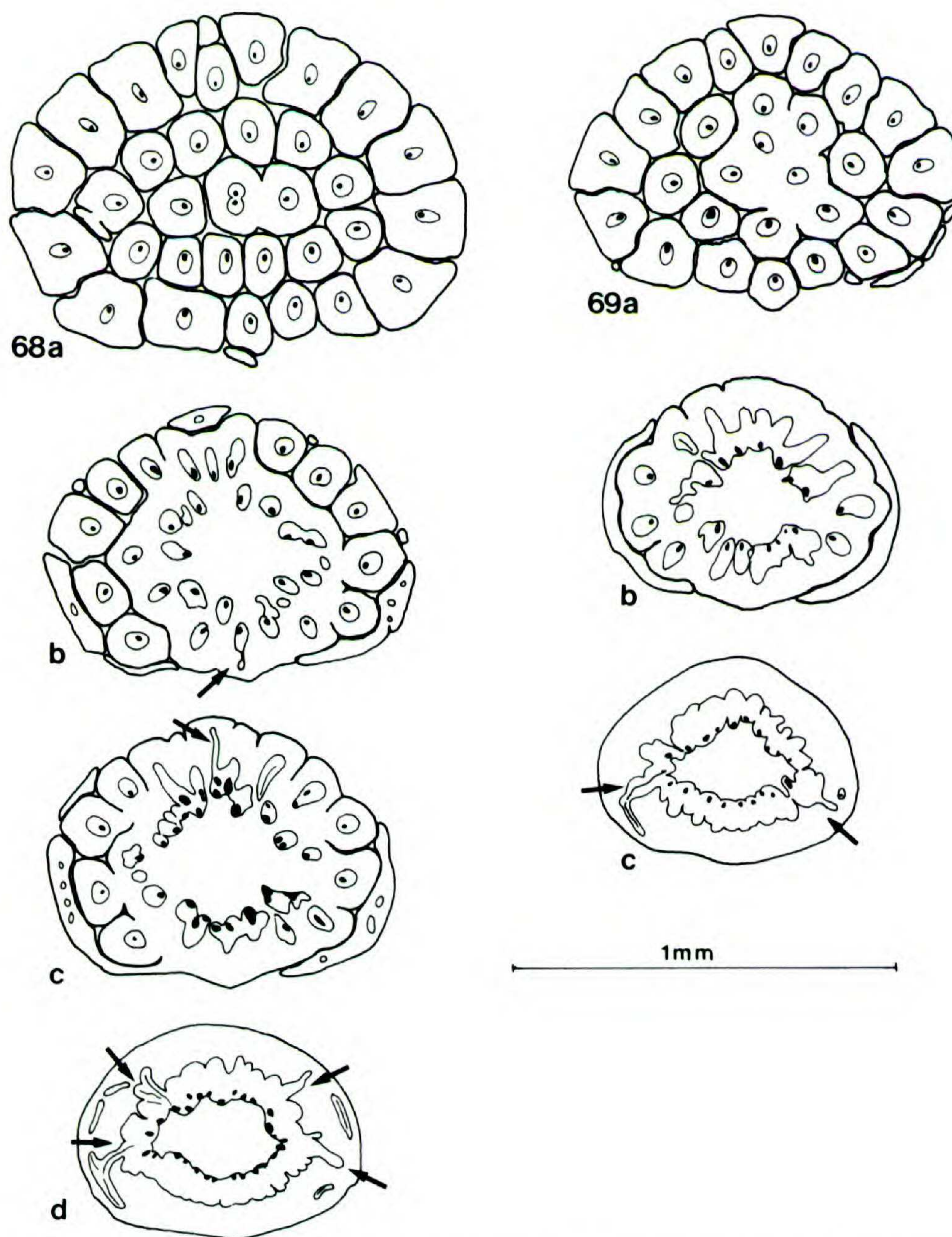
In addition, the tissues of the anthetic floral organs of both *Tetracentron* and *Trochodendron* are heavily tanniferous (Figs. 54, 55, 70, 71), but



FIGURES 56–61. 56, 57. *Trochodendron aralioides*. Flowers of a young inflorescence (August) from above.—56. Lateral zygomorphic flower, $\times 55$.—57. Terminal radially symmetric flower, $\times 40$. 58, 59. *Euptelea polyandra* (July).—58. Young inflorescence from above, floral pherophylls removed to show floral primordia, $\times 30$.—59. Same, enlarged; one zygomorphic flower with stamen primordia (larger on adaxial side), $\times 110$. 60, 61. *Cercidiphyllum japonicum*. Young female inflorescence (July) with three unisexual flowers, the carpel clefts oriented towards their pherophylls.—60. From above, $\times 120$.—61. From the abaxial side, median carpel (flower) without pherophyll, $\times 110$.



FIGURES 62-67. *Cercidiphyllum japonicum*. Young male inflorescences (July).—62. Very young stage, from above, perianth and first stamen primordia visible, abaxial side towards top, $\times 140$. 63-67. Somewhat older stage, viewed from different sides.—63. From above, abaxial side towards top, $\times 90$.—64. From the abaxial side, $\times 85$.—65. From the adaxial side, $\times 90$.—66. From lateral (right side of Fig. 63), $\times 80$.—67. From lateral (left side of Fig. 63), $\times 90$.



FIGURES 68, 69. *Cercidiphyllum japonicum*. Young male inflorescences, series of transverse sections.—68. Inflorescence with pherophylls on adaxial and abaxial sides: a, level with uppermost stamens becoming free from floral base; b, vascular trace of pherophyll of abaxial side joining a stamen bundle (arrow); c, vascular trace of pherophyll of adaxial side joining a stamen bundle (arrow); d, vascular traces of lateral pherophylls joining vascular stele of inflorescence (arrows).—69. Inflorescence without pherophylls on median side: a, level with uppermost stamens becoming free from floral base; b, level of free lateral pherophylls; c, vascular traces of lateral pherophylls joining vascular stele of inflorescence (arrows).

less so in *Euptelea* and *Cercidiphyllum*. A high tannin content is also typical for the flowers of Hamamelidales and many Magnoliales.

CONCLUSIONS

CIRCUMSCRIPTION OF TROCHODENDRALES

From our present knowledge it is evident that Trochodendrales sensu lato (including *Trochodendron*, *Tetracentron*, *Euptelea*, and *Cercidiphyllum*) are clearly related and form a coherent group because in none of the four genera can a relative be found in another order that would be

more close than any of the three other genera. It is true that the extremes are relatively far apart. There is a relatively large step in floral structure between *Tetracentron* and *Cercidiphyllum*. However, in vegetative morphology the two genera resemble each other so much that the relationship is instantaneously evident. Furthermore, the meristic variation in floral organs is a typical constitutive feature of primitive angiosperms. The range in floral structure within the four genera is of about the same level as within the Hamamelidales sensu stricto (Hamamelidaceae, Platanaceae, possibly Myrothamnaceae). Therefore,



FIGURES 70, 71. "Oil" cells in floral tissue.—70. *Tetracentron sinense*; longitudinal section of old floral bud, "oil" cells present in all organs, $\times 55$.—71. *Trochodendron aralioides*; transverse section of ovary at anthesis, $\times 140$.

the four genera are formally best treated as an order Trochodendrales (like Dahlgren, 1980, but not 1983).

CLASSIFICATION OF THE TROCHODENDRALES

Of the four extant genera, *Trochodendron* and *Tetracentron* are the two most closely related. The present investigation shows that they are much more similar than has been pointed out earlier. This is reflected in Table 1. The most distinctive resemblances include: occurrence of a perianth (although rudimentary in *Trochodendron*), markedly valvate anther dehiscence, presence of a nectary on the carpellary dorsal bulges containing many sunken stomata surrounded by a ring of epidermal cells with heavily sculptured cuticle (all new characters); additionally, the very similar and distinctive pollen, ovaries and ovules, fruits and seeds, and also the similar vesselless wood and similar stomata in the vegetative body (Bondeson, 1952; Baranowa, 1983).

All this strongly points to the inclusion of both genera, *Trochodendron* and *Tetracentron*, in the same family Trochodendraceae (as suggested earlier by Gundersen, 1950, or—before the inflation of taxonomic group numbers on all hierarchic levels—by Hallier, 1903b: Trochodendreae of Hamamelidaceae). The remaining two genera of the order, *Euptelea* and *Cercidiphyllum*, may remain in separate families. Therefore, for the moment, a fairly balanced classification of the group would be as follows:

Trochodendrales	
Trochodendraceae	<i>Trochodendron</i> <i>Tetracentron</i>

Eupteleaceae	<i>Euptelea</i>
Cercidiphyllaceae	<i>Cercidiphyllum</i>

FOSSIL RECORD OF THE TROCHODENDRALES

Today, all four genera of the Trochodendrales are restricted to more or less small areas in temperate or subtropical Eastern Asia from Nepal (*Tetracentron*) to Taiwan (*Trochodendron*) and Japan (*Cercidiphyllum*, *Euptelea*, *Trochodendron*).

Cercidiphyllum was widely distributed in the Northern Hemisphere in the Tertiary (newer finds and reviews, e.g., Brown, 1962; Hummel, 1971; Becker, 1973; Chandrasekharan, 1974; Iljinskaja, 1974; Jähnichen et al., 1980; Scott & Wheeler, 1982; Basinger & Dilcher, 1983; Hickey et al., 1983; Stockey & Crane, 1983) and perhaps back to the Upper Cretaceous (Maestrichtian) (Hickey et al., 1983). In the Paleocene other genera were affiliated with *Cercidiphyllum*, such as *Joffrea* (Crane & Stockey, 1985) and with less certainty *Jenkinsella* (Chandler, 1964; Crane, 1978). Retallack and Dilcher (1981) even pointed to similarities between early *Cercidiphyllum* and the mid-Cretaceous genus *Prisca*.

Fossils of the three other genera can be identified with less certainty. Fossil leaves have been compared (with doubts) with *Trochodendron* and *Tetracentron* as far back as to the mid-Cretaceous (Iljinskaja, 1972, 1974). *Tetracentron*-like wood has been described from the Upper Cretaceous (Page, 1968). Wood ascribed to *Euptelea* was found in the early Tertiary of North America (survey in Wolfe, 1973).

The combined presence of leaves, fruits, and seeds of *Cercidiphyllum* in various fossil beds

TABLE 1. Character states occurring in more than one but not in all genera of the Trochodendrales to show their relationships.

<i>Tetracentron</i>	<i>Trochodendron</i>	<i>Euptelea</i>	<i>Cercidiphyllum</i>
entomophilous nectaries on carpel dorsal surface short anthers, short connective tips anther dehiscence markedly valvate pollen 10–15 μ m diam. exine striate-rugulate apertures (colpi) long ovules mature at anthesis carpels sessile gynoecium syncarpous ovary semi-inferior seed coat 5-layered, middle layer sclerified phyllomes between prophylls and stamens present (tepals) floral prophylls regularly present “oil” cells present in floral organs wood without vessels		anemophilous nectaries lacking long anthers, long connective tips anther dehiscence longitudinal or slightly valvate pollen 20–30 μ m diam. exine finely reticulate and scabrate apertures short ovules immature at anthesis carpels stipitate gynoecium apocarpous or unilocarpellate ovary superior seed coat multilayered phyllomes between prophylls and stamens lacking floral prophylls lacking or present in basal flowers only “oil” cells lacking wood with vessels	
carpels weakly peltate		carpels strongly peltate	carpels epeltate
pollen triaperturate fruits dehiscent seeds with appendages		pollen pluriaperturate fruits indehiscent seeds without appendages	pollen triaperturate fruits dehiscent seeds with appendages
flowers bisexual leaves alternate			flowers unisexual leaves opposite
stamens 4 flowers enclosed by perianth in bud carpels 4	stamens numerous flowers enclosed by cataphylls in bud		
flowers sessile stipules present 1-leaved short shoots present	carpels numerous flowers pedicelled stipules absent 1-leaved short shoots lacking		carpel 1 flowers sessile stipules present 1-leaved short shoots present
leaves deciduous	leaves evergreen	leaves deciduous	

TABLE 2. Character states of the Trochodendrales shared with certain Magnoliidae or Hamamelidae to show their relationships. Some of the character states occur in both subclasses but are more important on the side where they are mentioned. The initials of the genera of Trochodendrales are mentioned in brackets if a feature does not occur in the other ones (C, *Cercidiphyllum*; E, *Euptelea*; Te, *Tetracentron*; Tr, *Trochodendron*).

Magnoliidae	Trochodendrales	Hamamelidae
<div><div><div>carpel number with wide range</div><div>carpel stipitate, style lacking (E)</div><div>nectary on carpel dorsal surface (Te, Tr)</div><div>stigma with unicellular papillae</div><div>wood vesselless (Te, Tr)</div><div>“oil” cells present (Te, Tr)</div><div>single adaxial prophyll (C)</div><div>chloranthoid leaf teeth (Te, Tr, C)¹</div><div>plants more or less glabrous</div><div>lack of myricetin²</div></div><div><div>anther dehiscence valvate (Te, Tr, E)</div><div>filaments long</div><div>pollen tri- or pluriaperturate with marked apertural exine structure</div><div>ovary semi-inferior (Te, Tr)</div><div>ovules immature at anthesis (E, C)</div><div>fruits dehiscing, seeds edged and winged (Te, Tr, C)</div><div>presence of an unelaborated compitum in syncarpous taxa (Te, Tr)</div><div>stipules present (Te, C)</div></div></div>		

¹ Hickey and Wolfe (1975).
² Kubitzki and Reznik (1966).

facilitates the identification of the material. That the fruits and seeds of *Cercidiphyllum* are better suited to fossil preservation than those of the other three genera is probably due to their more robust texture and flat shape limiting deformation.

All these many finds, especially those of *Cercidiphyllum* and extinct genera related to it with an obviously much wider distribution and greater diversification in the early Tertiary corroborate the impression that the Trochodendrales are a relic group with a long history, and are now in the state approaching extinction. Present modest diversity on the generic level (*Euptelea* and *Cercidiphyllum* with two species each) points to relatively recent differentiations.

POSITION OF THE TROCHODENDRALES BETWEEN
THE MAGNOLIIDAE AND HAMAMELIDAE

The Trochodendrales are closely related to Magnoliales and at the same time to Hamamelidales. The Trochodendrales are intermediate between the core Magnoliidae and Rosidae/Ham-

amelidae (Table 2): Some have retained vesselless wood and “oil” cells, but they have already acquired tricolpate pollen and valvate anthers of a hamamelidalian type. The odd female flowers of *Cercidiphyllum* consisting of a single carpel fall rather in the range of Magnoliidae than Hamamelidae. The distance to the core Magnoliales and Hamamelidales is about the same for all four genera, but for each from different angles. Additional embryological features not mentioned in the text, sieve tube plastid differentiation or chromosome numbers do not contribute much to this special question because they are too uniform in the critical groups under consideration here (Yakovlev, 1981; Ly-thi-Ba, 1981; Behnke, 1981) or too diverse (Ratter & Milne, 1973, 1976).

The perianth may be seen as a marker trait. In the Magnoliales the perianth is not yet differentiated into typical sepals and petals (cf. Hiepko, 1965). In the Trochodendrales the perianth is reduced, whereas in the Rosales/Hamamelidales it is often differentiated into sepals and petals, sometimes also reduced (at least partly

from a double perianth, cf. Endress, 1977; see also Ehrendorfer, 1977).

It seems reasonable that the Trochodendrales evolved from an ancestral group which had a perianth, but not yet differentiated into sepals and petals, as in Magnoliales. The Hamamelidales, in contrast, originated from a group where a well-differentiated perianth with sepals and petals already occurred, but petals *and* sepals were secondarily lost in many taxa.

On the whole, the Trochodendrales are not ancestral to the Hamamelidales. They are a conservative, isolated group. However, they have common roots with Hamamelidales and have retained more magnolialian traits than have the Hamamelidales.

Therefore, the formal inclusion of Trochodendrales in either Magnoliidae or Hamamelidae can be justified. An inclusion in the Hamamelidae seems reasonable (if this subclass is retained as such at all) because it is a smaller subclass than Magnoliidae.

The urgent need now is a detailed comparative study of all families of Magnoliidae and Hamamelidae, and not a premature phenetic or cladistic classification solely from the available information in the literature. Our ultimate goal is better knowledge of the living plants and better understanding of their phylogeny.

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